10

The Role of Herbivores in Grasslands

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The view that "grassland communities are determined by climate and soil" is the most commonly held paradigm concerning the origin and distribution of the grassland vegetation type (Coupland, 1979; French, 1979). Yet evidence is accumulating that interactions among herbivores and producers are also significant in determining the boundaries of grasslands (Harper, 1977). The primary interaction concerns the effects of defoliation on primary production (Marshall and Sagar, 1968; Chew, 1974). Defoliation by herbivores may not always be as detrimental as is typically supposed. If herbivory does, in fact, have salutary effects on production, then ecologists and range managers need to consider how consumers affect the transfer of energy in other than the linear fashion depicted in most models of grassland ecosystems (recently summarized by Redetzke and Van Dyne, 1979). We introduce some questions, pertinent data, and hypothetical formulations as a challenge to the long-standing notions about producer-consumer (vertebrate and invertebrate) interactions that have historically been used to define grassland community function.

Although the literature concerning herbivore impact on grasslands is abundant and varied, spatial and temporal relationships have received far too little consideration. We feel this has led to incomplete conclusions that are sometimes conflicting and often erroneous; yet those conclusions comprise the information base used to derive current models of the grassland ecosystem. The deficiencies became increasingly apparent as we organized the information in a hierarchical fashion—from biochemical processes of individual plants and animals to ecosystem function. The employment of hierarchical logic on both temporal and spatial scales proved to be a most challenging task, but in the process we have revealed counterintuitive phenomena among plant-herbivore interactions, most notably a significant increase in photosynthetic rate of grazed plants. It is these counterintuitive events we wish to address.

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THE GRASSLAND SYSTEM

Producers

Grasslands cover approximately 25% of the world's land surface (Shantz, 1954), typically occupying regions receiving 250–1,000 mm of annual precipitation and having mean annual temperatures of 0–20°C (Lauenroth, 1979). Lauenroth (1979) found that slightly over half of the variation in aboveground net primary production (ANPP, $g.m^{-2}$) among 52 grassland sites around the world could be accounted for by the equation

$$\text{ANPP} = 0.5\ \text{PPT} - 29 \qquad (1)$$

where PPT is annual precipitation (mm). Similarly, Sims and Singh (1978b) reported that annual precipitation accounted for 46% and 58% of the variability in total NPP of ungrazed and grazed North American grasslands, respectively. Leaf elongation and photosynthesis are among the processes that are most sensitive to water stress (Boyer, 1970; Detling, 1979). The effects of water stress on these processes in two important North American mixed-grass and shortgrass prairie species (*Bouteloua gracilis*, a C_4-photosynthetic pathway species, and *Agropyron smithii*, a C_3-species) are shown in Figure 1. These results, based on data of Majerus (1975) and Brown and Trlica (1974, 1977), suggest that water stress not only inhibits net photosynthesis but is even more effective in inhibiting leaf surface area. Even though other factors, such as soil nutrients (Dodd and Lauenroth, 1979), are important in governing grassland primary production, the interaction of water and herbivores may frequently be the most significant factor controlling grassland productivity (McNaughton, 1979).

Grazing affects a variety of structural and functional characteristics of grasslands. Sims *et al.* (1978) analyzed primary production data from grazed and ungrazed North American grassland sites studied during the International Biological Program (IBP) Grassland Biome Project, and their analysis revealed interesting trends in the percentage contribution of various plant functional groups (Figure 1). For example, cattle grazing at the Northern Mixed-Grass Prairie Site at Cottonwood, South Dakota, resulted in a dramatic shift from a predominance (78%) of cool-season (C_3-photosynthetic pathway) grasses to a predominance (74%) of warm-season (C_4-photosynthetic pathway) grasses. By contrast, cattle grazing at the shortgrass sites in Colorado and Texas led to slight decreases in percent-

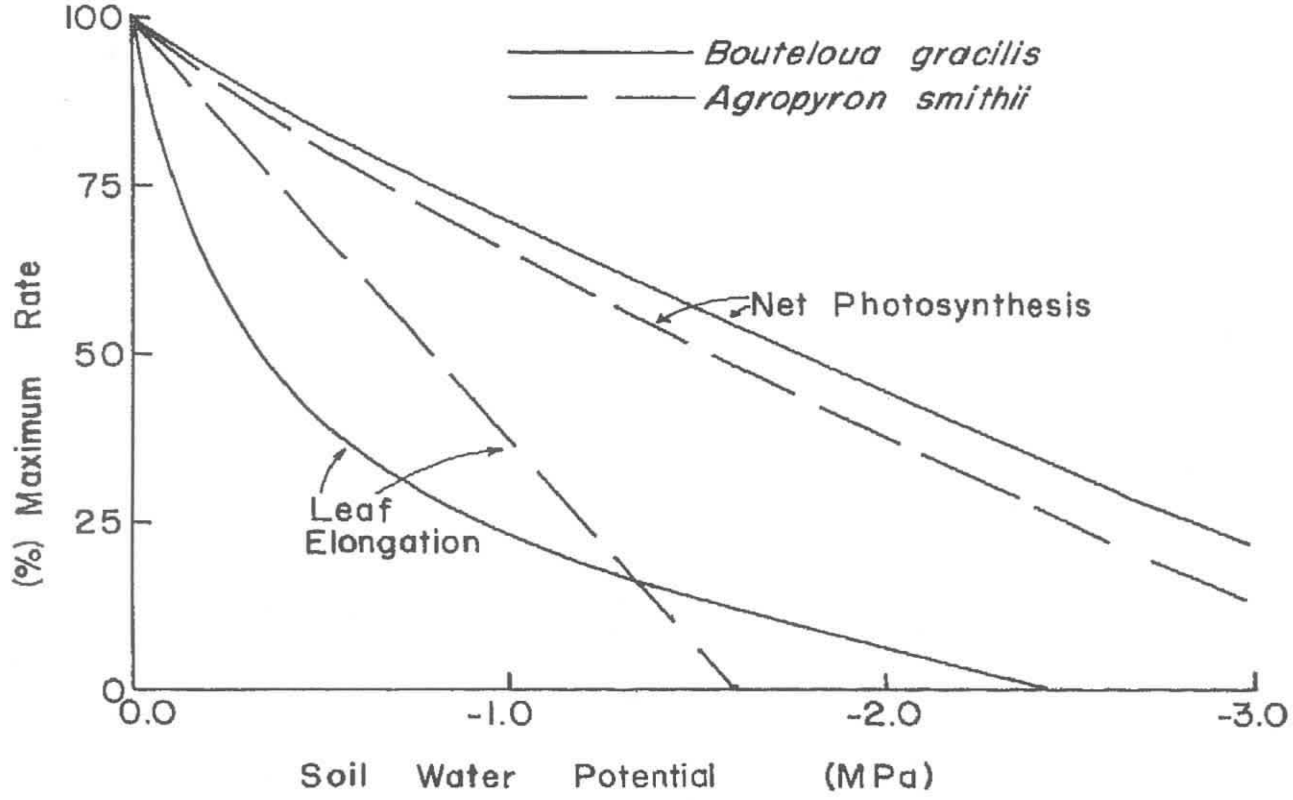

FIGURE 1. Relationship among soil water potential, net photosynthesis, and leaf elongation rates of *Bouteloua gracilis* (C_4) and *Agropyron smithii* (C_3) from North American mixed-grass and shortgrass prairies. Curves are based on CO_2 exchange data of Brown and Trlica (1974, 1977) and leaf growth data of Majerus (1975).

age composition of all of the plant functional groups except CAM-succulents, which nearly doubled in percentage. Similarly, grazing caused forbs to increase in importance at the Tallgrass Prairie Site (Osage, Oklahoma) and the Desert Grassland Site (Jornada, New Mexico). However, relative plant functional-group composition was unaffected at the Shrub-Steppe Site (northwest bunchgrass near Richland, Washington). Sims *et al.* (1978) concluded that sites with <10°C mean annual temperature showed a marked shift to warm-season plants as a result of grazing, while those with >10°C mean annual temperature showed only a slight increase in warm-season plants (Figure 1).

The ten North American grasslands examined by Sims and Singh (1978b) had average ANPP values of 212 $g.m^{-2}/yr^{-1}$, only 10% less than ANPP at ungrazed sites (236 $g.m^{-2}/yr^{-1}$). The mean total-shoot standing crop, averaged across all ten grasslands, was higher in ungrazed treatments (245 $g.m^2$ than in grazed treatments (161 $g.m^2$) (Sims *et al.*, 1978). This was due principally to the greater amount of standing dead-plant material on the ungrazed treatments, as there were no significant differences in seasonal live-shoot biomass between grazed and ungrazed treatments (Sims and Singh, 1978a).

Consumers

Grassland consumer communities are, for the most, relatively simple in terms of diversity. This phenomenon is probably related to the relative lack of stratification in grassland communities. Despite the simple nature of grasslands, there is a large consumer biomass that is probably unequaled in other systems (McNaughton, 1979).

For grassland vertebrates there is a strong positive correlation between mean annual precipitation and estimated peak biomass (Figure 2). The exception is at the Mountain Grassland Site (near Bozeman, Montana) in the Rocky Mountains. Standing crop biomass at this site is indicative of a depauperate fauna, perhaps a result of severe winters. Grassland vegetation is known to be closely correlated with precipitation (Lauenroth, 1979); therefore, as expected, a strong positive correlation also exists between vertebrate consumer biomass and peak standing crop of plants (Figure 3). The Mountain Grassland Site again fails to fit the general scheme, though not as dramatically as for the climatic parameter.

Traditionally the consumer community has been partitioned into the aboveground invertebrate, belowground invertebrate, and vertebrate guilds. It is difficult to generalize standing-crop and production values of consumers because there is considerable variation from grassland to grassland. For instance, Dyer (unpubl.) has estimated peak standing levels of vertebrate consumer biomass of 86.99 kg/ha for the Tallgrass Prairie Site, 1.43 kg/ha for the Mountain Grassland Site, and 1.83 kg/ha for the Desert Grassland Site. The average consumer biomass for six North American grassland ecosystems (Tallgrass Prairie, Shortgrass Plains, Mixed-Grass Prairie, Desert Grassland, Mountain Grasslands, and Shrub-Steppe) is estimated to be 27.981 kg/ha if one includes large herbivores (primarily cattle) and 0.294 kg/ha if large herbivores are excluded. Invertebrate biomass estimates also vary, ranging from 0.69 kg/ha in the Desert Grassland to 2.80 kg/ha in the Shrub-Steppe. A mean estimate is 1.21 kg/ha for five grassland systems of North America (Scott and Leetham, unpubl.). These values ignore the belowground biomass.

Scott and Leetham (unpubl.) estimated soil microfauna biomass, excluding nematodes, to be 1.62 kg/ha in the Shortgrass Site and 13.22 kg/ha in the Tallgrass Prairie. In four grasslands (Shortgrass Plains, Mixed-Grass Prairie, Tallgrass Prairie, and Shrub-Steppe) average nematode peak biomass was estimated to be 16.73 kg/ha. In the Canadian Mixed-Grass Prairie of Saskatchewan (Coupland, 1979) total belowground invertebrate biomass was estimated to be 43.65 kg/ha.

Belowground consumer biomass for the investigated grasslands is then estimated as 52.13 kg/ha. Although this value is troublesome because of

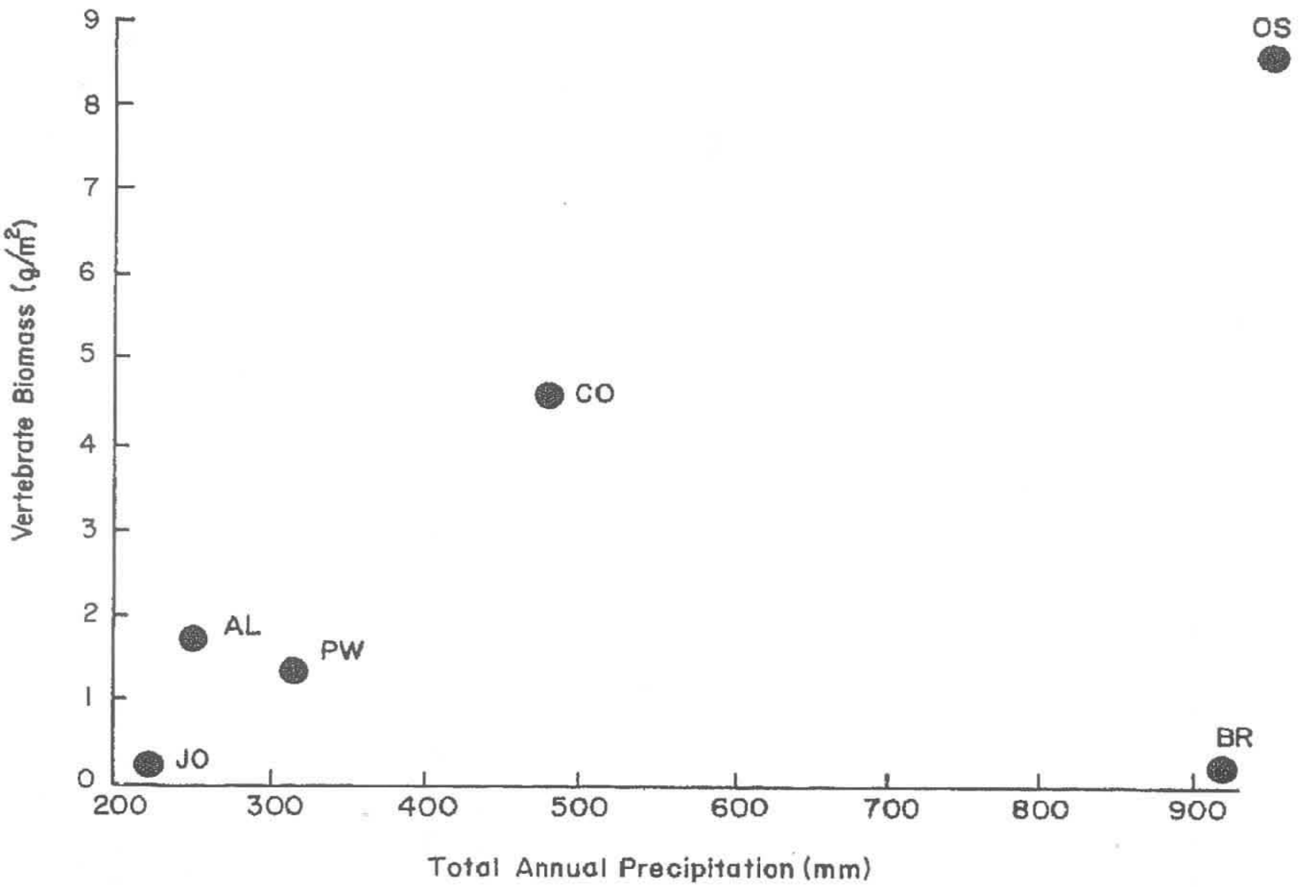

FIGURE 2. Relationship between the standing crop of vertebrates and total annual precipitation of North American grasslands. Units have been converted to dry weight. JO = Jornada, New Mexico, Desert Grasslands; AL = Richmond, Washington, Northwest Pacific Shrub Steppe; PW = Pawnee, Colorado, Short-Grass Prairie; CO = Cottonwood, South Dakota, Mixed-Grass Prairie; OS = Osage, Oklahoma, Tall-Grass Prairie; BR = Bozeman, Montana, Mountain Grasslands.

excessive averaging of highly varied ecosystems; it is the only value available.

What then is the total impact in terms of grazing? This proves to be a difficult problem to solve, for there is no convenient way to convert standing-crop biomass taken at peak periods without consideration of the dynamics of the various consumer populations; it is a feat seldom done. Nonetheless, by taking estimated consumption levels (ignoring saprophages and secondary consumers) for three of the four grasslands reported by Scott *et al.* (1979) and annual production reported for the same areas by Lauenroth (1979), we estimate that in Tallgrass Prairies the primary consumer fauna utilize 26% of the primary production, in Shortgrass Plains 30%, and in Mixed-Grass Prairies 55%. The remaining annual production is degraded by various microorganisms competing for the fixed carbon, or it goes into various subsystems for periods longer than an annual cycle

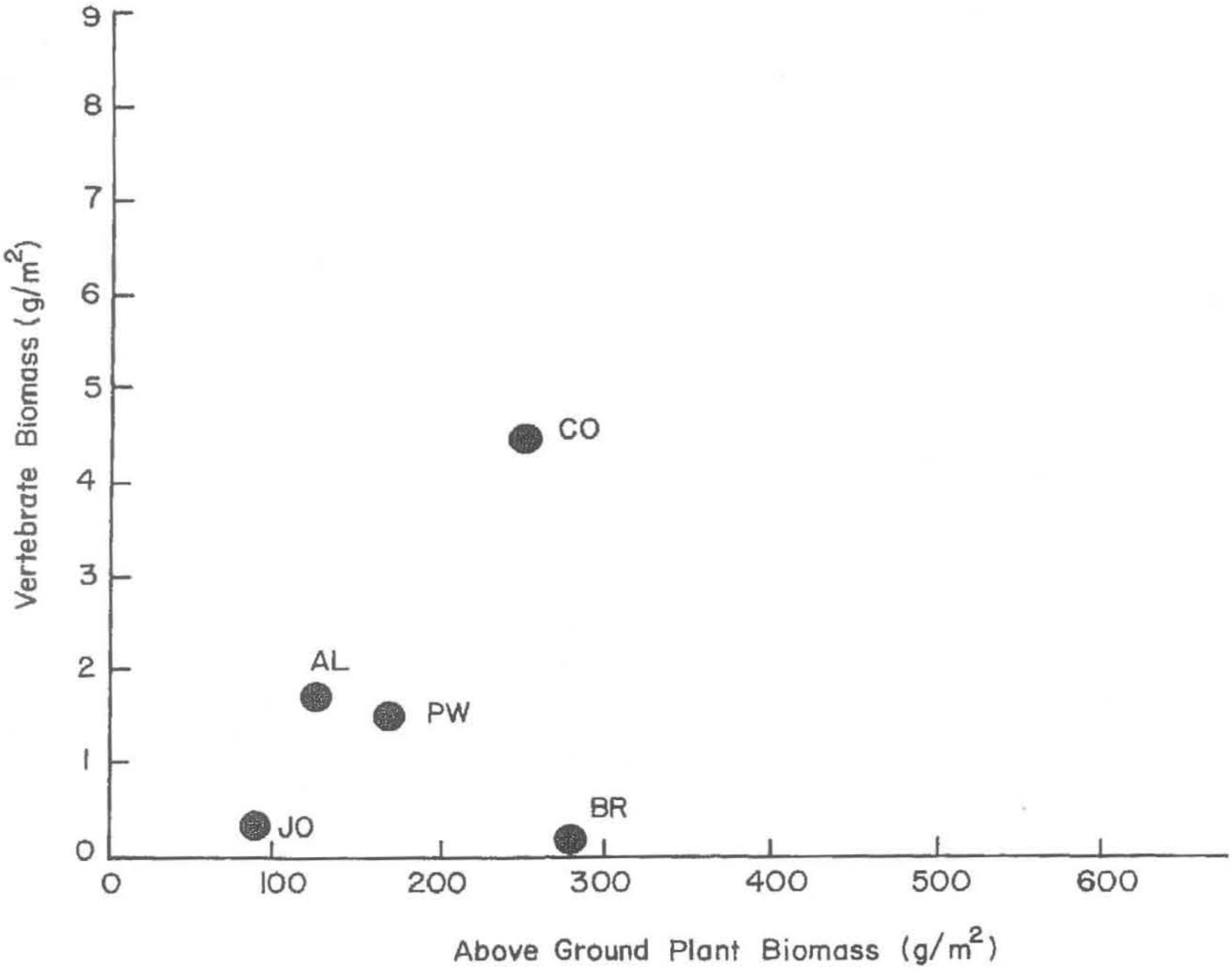

FIGURE 3. Relationship between the standing crop of vertebrates and aboveground herbage of North American grasslands. See Figure 2 for explanation of units and legend.

before it is ultimately degraded and oxidized by biological-physical features of the community. It is unfortunate that there are such limited data bases from which to draw conclusions, but the range of 25–50% utilization seems credible to us for total impact. Scott *et al.* (1979), however, report somewhat lower values than we do for these grasslands; clearly additional data are necessary before patterns can be inferred on a continental basis. Nevertheless, this provides a first approximation of the level of impact of herbivore consumption on the North American grasslands.

HERBIVORY AS A PROCESS

Herbivores may affect the producer community via either of two processes: (1) the mechanical removal of plant tissue (biomechanical) or (2) as vectors of biologically active substances or agents (biochemical). The former process appears relatively straightforward and is generally considered detrimental to the autotroph community; however, we submit that defoliation at certain levels may actually increase net primary production through time. The occurrence of the second, the biochemical process, is in some dispute, except for pathogenic transfer; it is poorly understood, if at all.

Compensation Mechanisms

McNaughton (1979) lists nine mechanisms involved within the herbivore-plant interaction that may compensate for plant tissue lost durng the herbivore process. They are (1) increase in photosynthetic rate in residual tissue, (2) reallocation of substrate within the plant, (3) increase in light penetration through a diminished canopy, (4) removal of less-functional tissue that still require resources, (5) reduction of leaf senescence rates, (6) redistribution of growth hormones, (7) enhancement of soil water conservation, (8) redistribution and recycling of nutrients, and (9) introduction of growth-promoting substrates.

Effect on Individual and Population Function: Biomechanical Effects

Herbivory typically involves mouthparts that are adapted to plant predation: snipping teeth or mandibles (e.g., Bovidae, such as cattle and bison; Equideae, such as horses, burros, and zebras; and Orthoptera, such as grasshoppers and katydids), a sucking proboscis (e.g., Diptera, or flies), a piercing stylet (e.g., Homoptera, such as aphids, whiteflies, and leafhoppers), or chewing mandibles permitting passage of the entire animal through the plant (e.g., Coleoptera, such as leaf miners). The primary herbivores are those with the snipping adaptation.

The removal of plant tissues and organs may be generalized or specialized with respect to taxa and tissue selected; however, many grazing effects can be simulated, if we consider these herbivores as mere "mowing machines" (Falk, 1976). The primary technical problem in experimental studies of herbivory is the simulation of grazing distribution through the plant community (spatial scale). Thus it is necessary to have accurate measures of (1) the numbers of animals feeding per unit area, (2) degree of taxon and tissue specificity, (3) repetition of visits, (4) biomass removed each visit, and (5) foraging pattern of the primary consumers through space and time, both diurnal and seasonal.

The physical removal of the different parts of the plant results in physiological modifications of photosynthesis, respiration, carbon translocation, growth, and phenology (Harper, 1977; McNaughton, 1979; McNaughton *et al.*, in this volume).

SHOOT GRAZING.

Photosynthetic Rate. When a major proportion of a plant's foliage is removed by large herbivores or by severe insect infestations, the photosynthetic rate in the remaining undamaged leaves frequently increases or declines less rapidly with age than the photosynthetic rate in similar leaves from nondefoliated plants. Painter and Detling (unpubl.) recently studied this phenomenon in western wheatgrass (*Agropyron smithii*) by removing 50% or 75% of the tillers at a height of 5 cm. Photosynthesis was measured immediately before and 30 min after defoliation in the youngest fully expanded leaf on an undamaged tiller and at 2-day intervals for the next 10 days. Following a small but consistent decline (6–7%) in net photosynthesis ($\mathbf{P}_N$) immediately after defoliation, net photosynthetic rates in the remaining leaves increased to a maximum on day 4 (Figure 4). On days 2–10, $\mathbf{P}_N$ of leaves from moderately and heavily defoliated plants averaged 106% and 114% of their pretreatment rates, respectively, while rates in control plants averaged 90% of their pretreatment rates over this period.

Similar trends have been observed in a variety of other grasses. For example, Gifford and Marshall (1973) removed all tillers except the main shoot of *Lolium multiflorum* and found that net photosynthesis of selected fully expanded main-shoot leaves increased about 15% within the first day and then remained relatively constant through day 10, while $\mathbf{P}_N$ rates of similar leaves on control plants declined steadily to about one-third of their initial rate during this time. Detling *et al.* (1979b) followed photosynthetic rates of entire shoot systems of 40-day-old *Bouteloua gracilis* plants over the 10-day period following clipping at a height of 4 cm above the crowns. This treatment removed about 60% of the leaf blades and 45% of the total shoot biomass. Immediately following treatment $\mathbf{P}_N$ rates of the remaining tissue were 60% lower than before (Figure 5). Because leaf sheaths generally have a lower photosynthetic capacity than leaf blades (Ludlow and Wilson, 1971; Youngner et al., 1976), and clipping effectively increased the sheath/blade ratio, the initial decline in $\mathbf{P}_N$ may have been the result of a change in the relative proportions of sheaths and blades rather than a decrease in CO_2-uptake rates in the remaining intact tissue. Three days after defoliation, $\mathbf{P}_N$ rates had increased to more than 120% of the rates of control plants, and they remained at about this level through the tenth day. The increased $\mathbf{P}_N$ rates (Figure 5) were attributed to increased photosynthetic capacity in the remaining tissues or in those tissues produced after defoliation rather than an increase in the blade /sheath ratio (Detling *et al.*, 1979b).

This type of response to severe defoliation is not restricted to grasses. Rates of $\mathbf{P}_N$ in stubble leaves of *Medicago sativa* more than doubled over

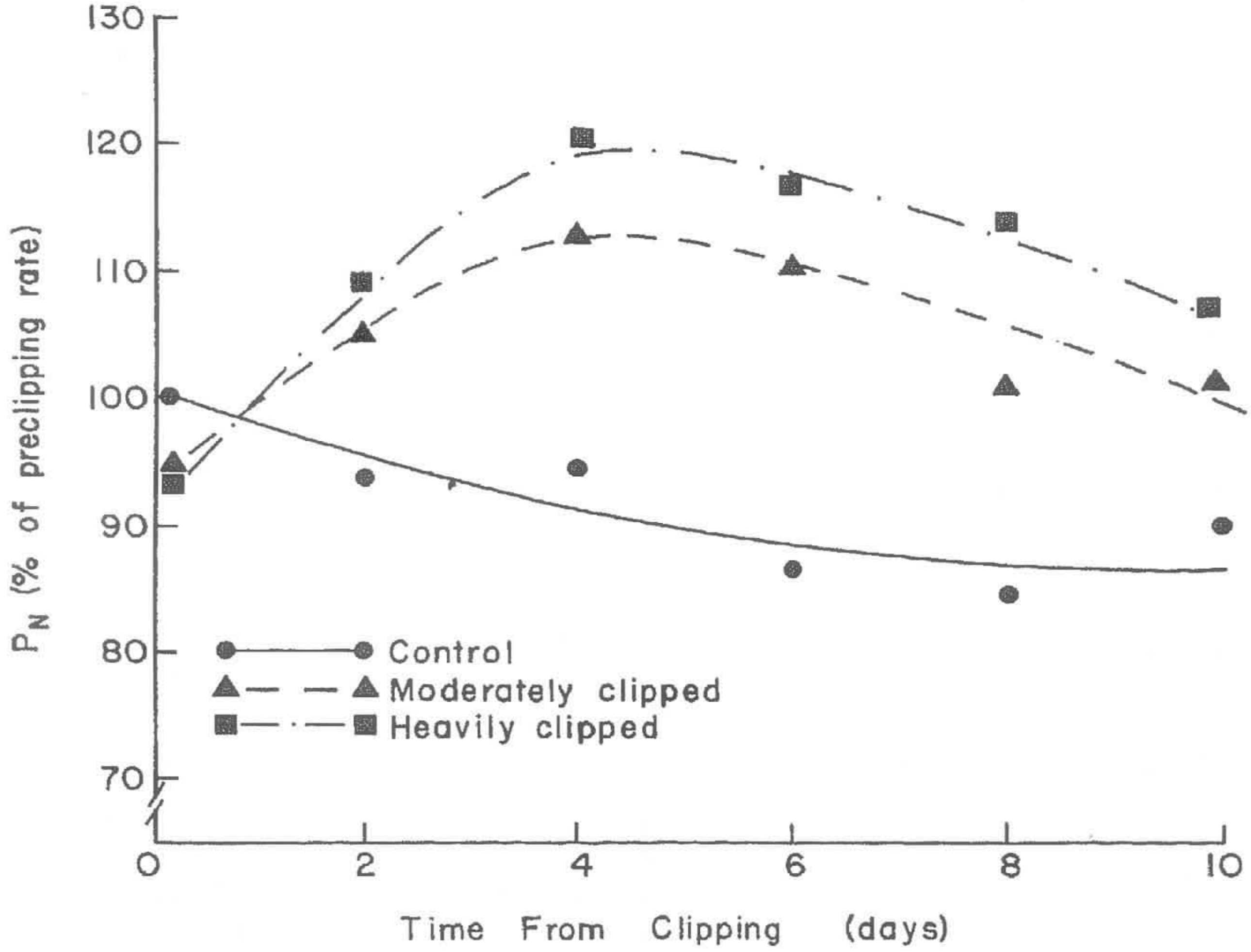

FIGURE 4. Effect of clipping on rates of net photosynthesis in an expanded leaf on an undamaged tiller of *Agropyron smithii* that had 50% to 75% of its tillers removed (Painter and Detling, unpubl.).

an 8-day period following defoliation to 15 cm above the stem base (Hodgkinson *et al.*, 1972; Hodgkinson, 1974). Similarly, partial defoliation led to increased P_N rates in remaining leaves of such diverse taxa as bean (Alderfer and Eagles, 1976), pine (Sweet and Wareing, 1966), and mulberry (Satoh *et al.*, 1977).

Exceptions to this trend have been reported. Ryle and Powell (1975) defoliated uniculm barley at the ligule of the third leaf. Rates of P_N in the two remaining fully expanded leaves were reduced 5–10% for up to two weeks. Moreover, P_N rates of newly formed leaves were not significantly different in defoliated and control plants.

Whereas photosynthesis of the remaining undamaged leaves of defoliated plants frequently is enhanced, P_N rates of the damaged leaves themselves are almost always reduced. McNary observed (unpubl.) the variety of feeding patterns of the grasshoppers *Aulocara elliotti* and *Ageneotettix deorum* on single leaves of western wheatgrass (Figure 6). Grasshopper grazing damage was then simulated by cutting similar notches from west-

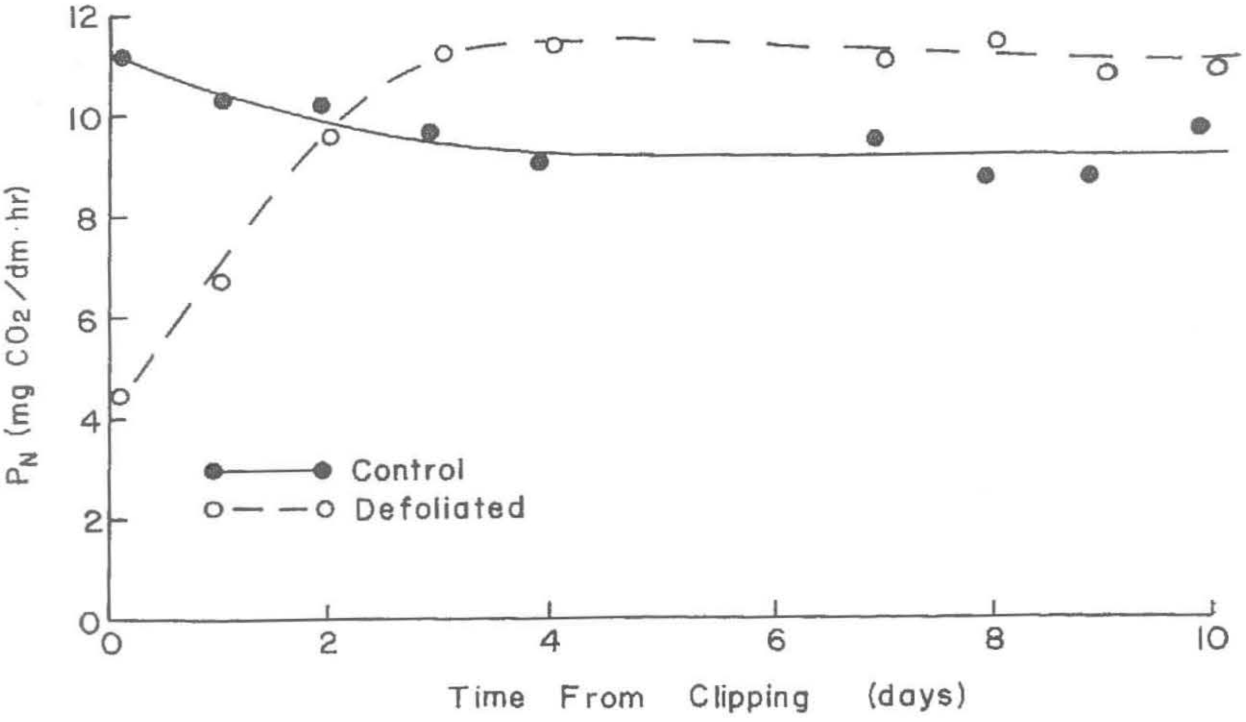

FIGURE 5. Rates of net photosynthesis in entire shoots of *Bouteloua gracilis* defoliated to a height of 4 cm (Detling *et al.*, 1980).

ern wheatgrass leaves. Net photosynthetic rates were monitored on the treated leaves immediately before and after cutting and periodically over the next six days (Detling *et al.*, 1979a). When notches were removed from both the base and apex of each blade (ca. 25% of the leaf area was removed) as in pattern 3b of Figure 6, $\mathbf{P}_N$ rates per unit of remaining leaf area were reduced by about 30% within an hour; they remained at that level for the next six days (Figure 7). Similar $\mathbf{P}_N$ reductions occurred (Figure 7) when a single notch was removed from the blade base (Figure 6, 2b) or when the distal ⅓ of the blade was severed (Fig. 6, 1b), but removal of a single notch from the tip of the blade had little impact on $\mathbf{P}_N$ (Figure 8). Reduction in $\mathbf{P}_N$ in leaves has been reported following feeding by spider mites (Hall and Ferree, 1975; Sances *et al.*, 1979) and insect-injury simulation (Hall and Ferree, 1976). Although some decrease in net photosynthesis of damaged leaves is probably attributable to injury-induced wound respiration (Macnicol, 1976), we observed no significant increases in respiration in either the light or dark (Figure 7).

Shoot Development. Aboveground, the rate of tiller production may be significantly affected by grazing. Youngner (1972) concluded that, when defoliation removes apices of elongated stems, apical dominance is broken and the rate of tiller production is increased. However, defoliation that removes only leaves usually leads to decreased tillering (Youngner *et al.*, 1976; Ackerson and Chilcote, 1978). This is because available carbo-

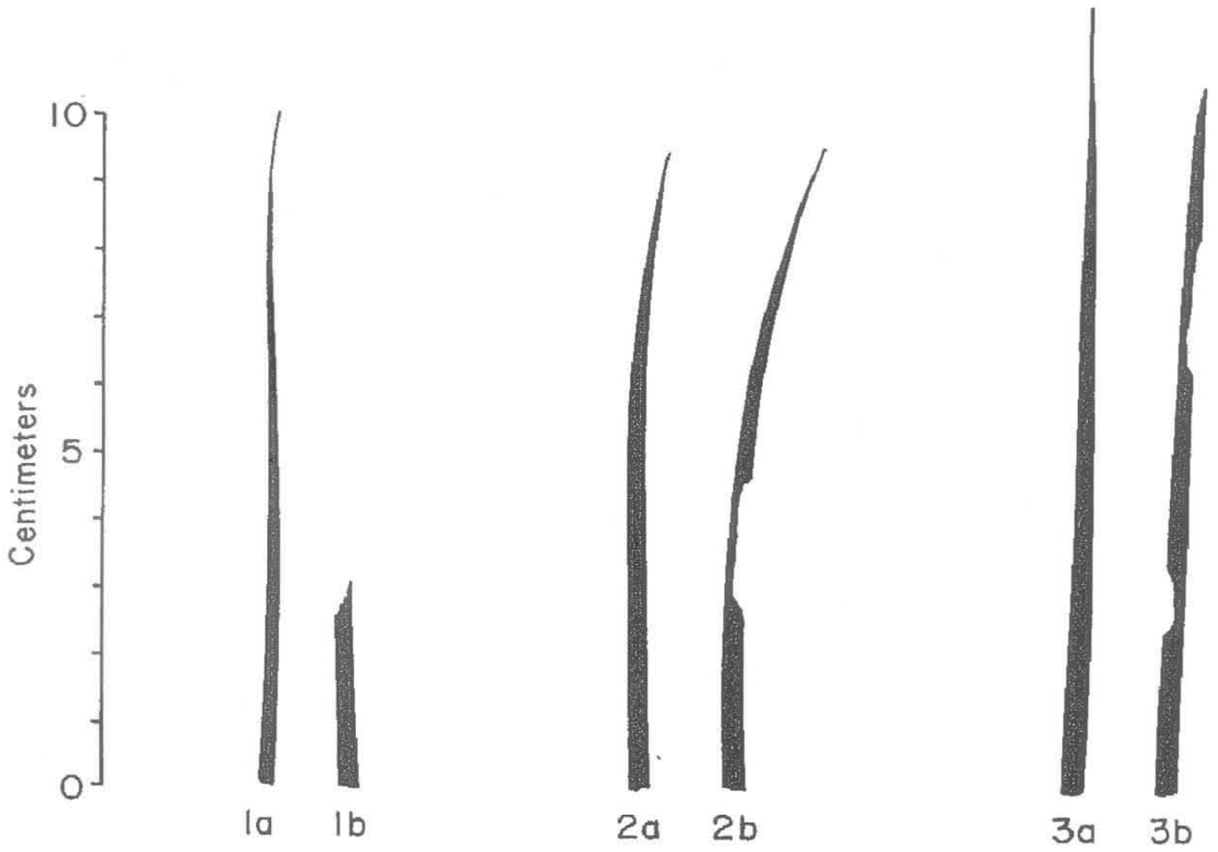

FIGURE 6. Typical grasshopper feeding patterns on leaves of *Agropyron smithii* (McNary, unpubl.).

hydrate is generally used for leaf growth on existing tillers before being used to support new tiller growth (Youngner, 1972). In closed canopies under field conditions, however, defoliation of grasses may enhance tillering even when stem apices remained undamaged. This could result from reduced shading and creation of a more favorable light environment (Youngner, 1972), which would be expected to stimulate tillering (Laude, 1972).

Root Development. Some of the most striking plant responses to defoliation are observed in belowground structures. Davidson and Milthorpe (1966) observed root elongation and respiration rates in *Dactylis glomerata* over an 8-day period following defoliation to a height of 2.5 cm. Root extension declined almost immediately and remained at only 1% of pretreatment rates before gradually increasing to 5% of pretreatment rates by day 8. Root respiration declined steadily to 25% of preclipping rates over the eight days. In addition, root mortality usually increases and root branching declines following defoliation (Hodgkinson and Baas-Becking, 1977; Evans, 1973a, b).

Translocation of Carbon Assimilates. In addition to a decrease in photosynthetic production that results from decreases in the canopy leaf area

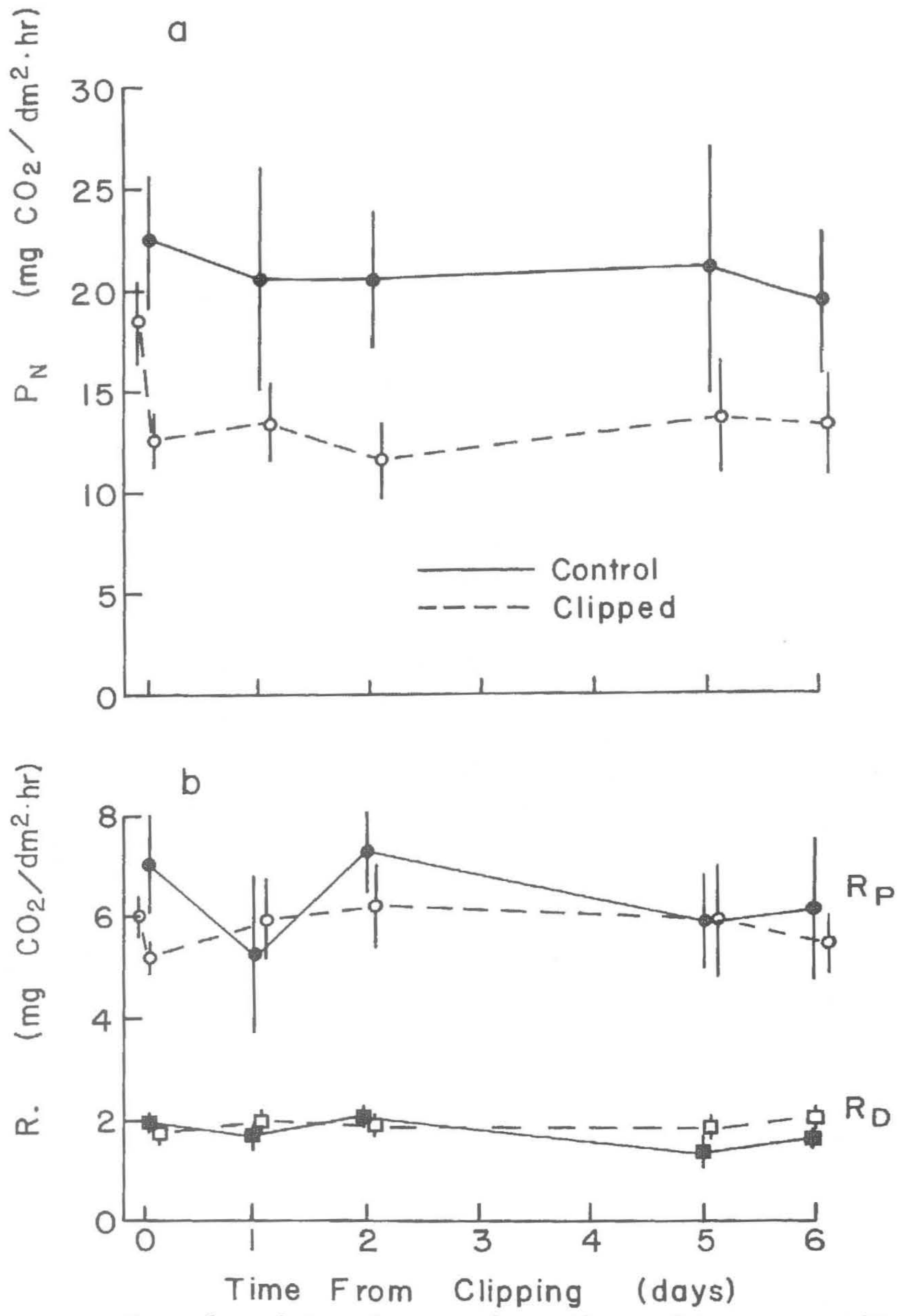

FIGURE 7. Rates of net photosynthesis in individual leaves of *Agropyron smithii* from which 4-cm-long pieces were removed from both base and tip end (Detling *et al.*, 1979a).

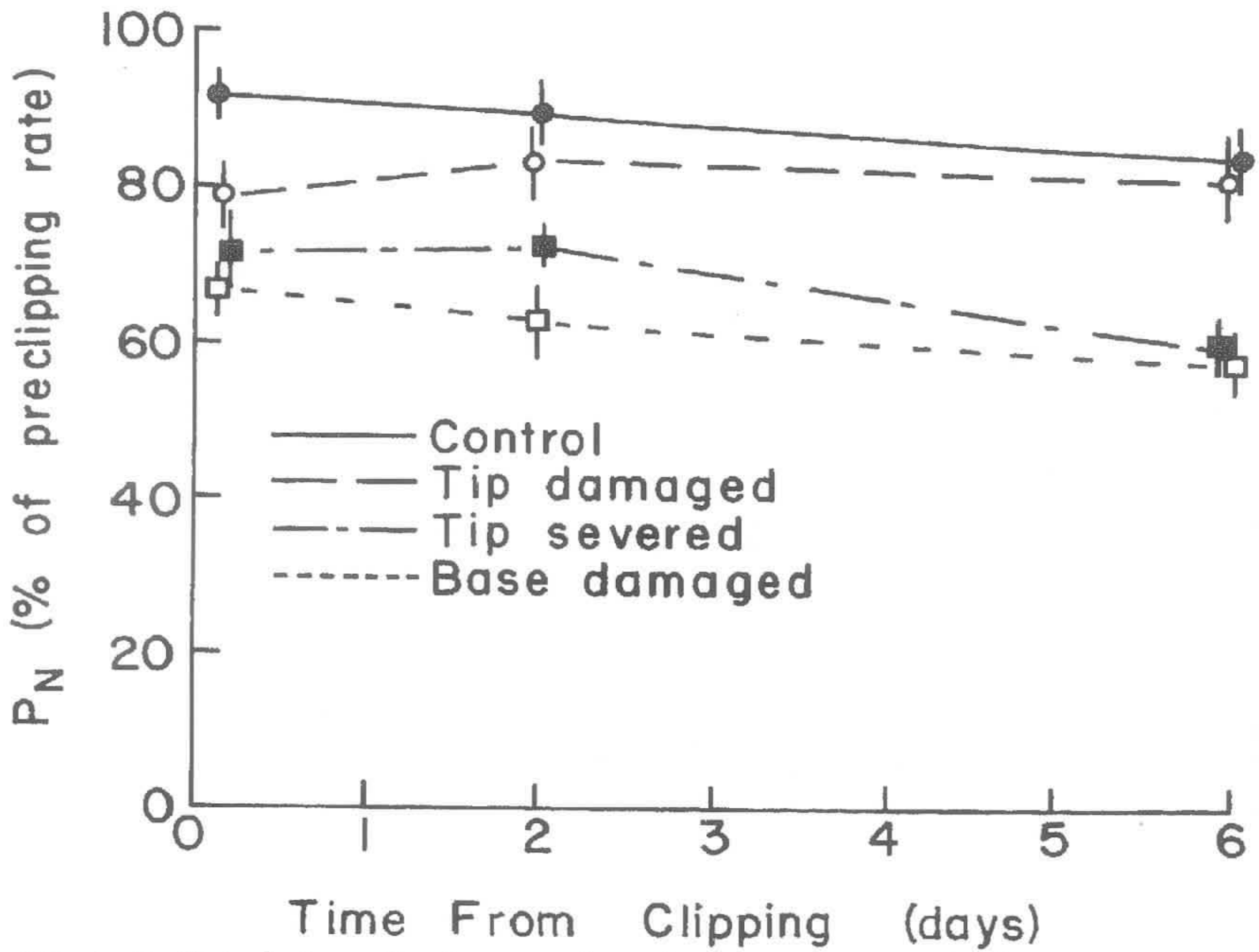

FIGURE 8. Net photosynthetic rates of single *Agropyron smithii* leaves treated in various ways to simulate grasshopper grazing (Detling *et al.*, 1979a).

and often from temporary decreases in photosynthetic rates (Detling *et al.*, 1979; Detling *et al.*, 1980), there is frequently a decline in the proportion of assimilates translocated to roots (Marshall and Sagar, 1965, 1968). As indicated by our results with *Bouteloua gracilis* defoliated at various heights, the proportion of photosynthetically assimilated ^{14}C translocated to roots declines with increasingly severe defoliation (Figure 9). Gifford and Marshall (1973) and Ryle and Powell (1975) have demonstrated that the assimilates were diverted from roots to rapidly regrowing shoot meristems. Thus tillers are photosynthetically independent in the ungrazed condition, but grazed tillers frequently become dependent upon connected, ungrazed tillers for photosynthate used in regrowth.

ROOT GRAZING. Recent studies of Smolik (1974), Coleman *et al.* (1976), Boyd and Perry (1970), Johnson and Burton (1973), and Stanton *et al.* (unpubl.) show that phytophagous nematodes are important in grassland ecosystems and that perhaps they are even the principal biophagic consumers, and that aboveground production is greatly affected by nematode grazing. Some evidence suggests that, when roots are infected with nema-

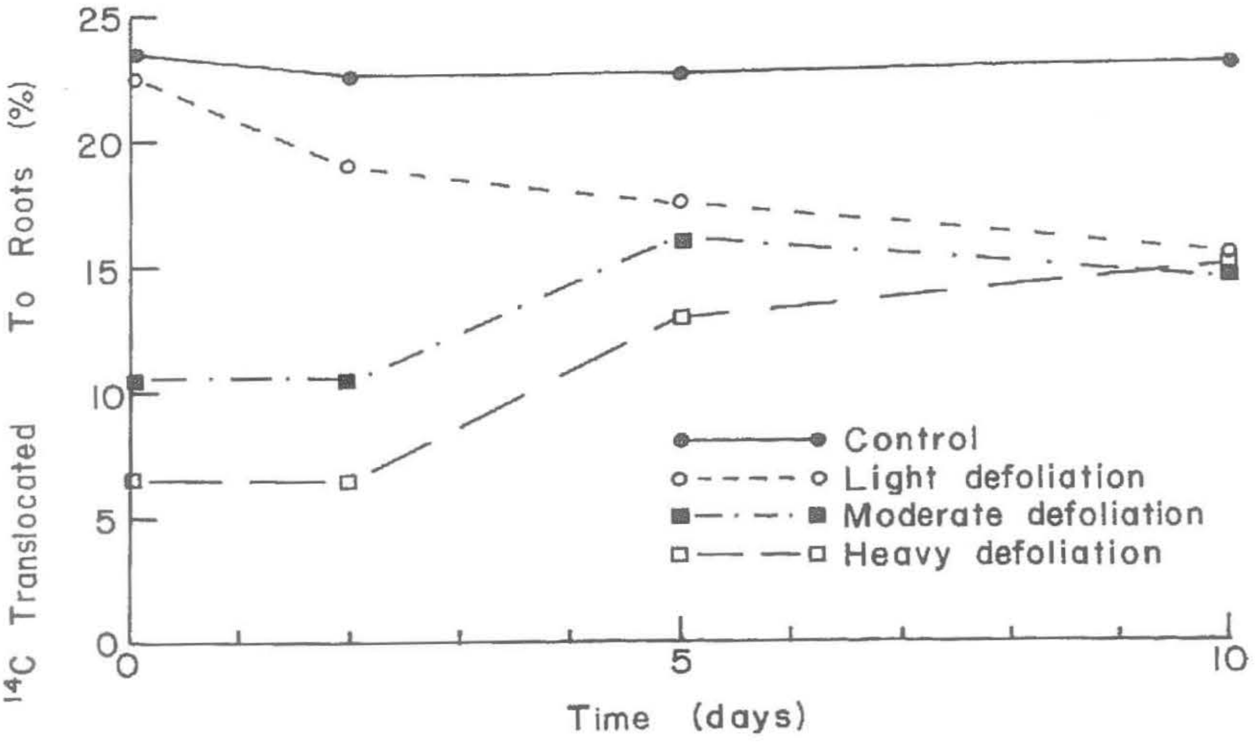

FIGURE 9. Allocation of photosynthetically fixed ^{14}C to roots (% of total fixed ^{14}C) of *Bouteloua gracilis* at various times following defoliation (Detling *et al.*, unpubl.).

todes, photosynthesis is decreased (Wallace, 1974). In a simulation experiment Detling *et al.* (unpubl.) measured $\mathbf{P}_N$ of single leaves of hydroponically grown *Bouteloua gracilis* over ten days following removal of all roots below 5 cm, about one-third of the root biomass. While there was day-to-day variation within each treatment, $\mathbf{P}_N$ of root-clipped plants averaged about 73% of the $\mathbf{P}_N$ of the controls for the first week following treatment (Figure 10). Smolik (1974) found that markedly reducing the nematode populations from soils resulted in an increase in aboveground production of about 30%. The parasitic nematode forms were decreased by 90%, while the saprophagic and predatory forms were decreased by 67–68%. The increase in aboveground production may result from physiological responses, such as increased nutrient and water uptake by the undamaged root biomass. Preliminary findings for tomato plants revealed that inhibition of upward translocation of water and nutrients may be more marked than alteration in photosynthetic CO_2 fixation in nematode-infected plants (Wallace, 1974); however, as noted by Seinhorst (1961), attributing all of the increased productivity to the removal of nematodes would be questionable. The mechanism of biophagic feedback on a plant population remains only partially understood, and the implications over ecological time of drastic reductions in nematode saprophages and predators by broad-spectrum nematocides is yet to be determined.

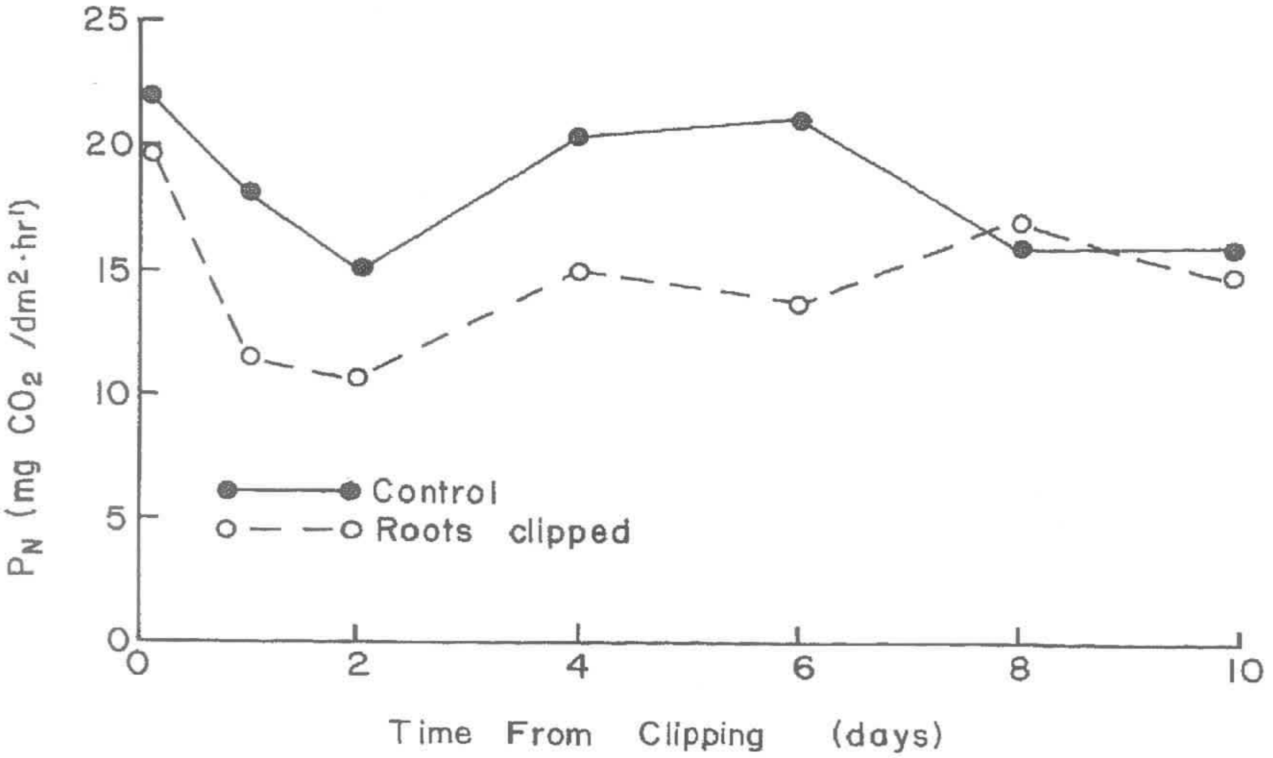

FIGURE 10. Net photosynthetic rates in single leaves of *Bouteloua gracilis* from which about ⅓ of the root biomass had been removed on Day 0 (Detling *et al.*, unpubl.).

Because the microenvironments are so heterogeneous in a field situation, various plant-parasitic nematodes may locate roots by responding to general cues of biochemical exudates, levels of carbon dioxide dissolved in water, negative electrical potentials, or heat of metabolism (Green, 1971). They may modify their behavior upon arrival at the root surface; such behavior was observed in the accumulation of the plant parasite *Hemicycliophora simulis* around the roots of several crop plants, including ryegrass (*Lolium perenne*) (Khera and Zuckerman, 1963). Most attractive to phytophagous nematodes are root hairs, root tips, and zones of elongation—all regions of considerable metabolic activity (Green, 1971). The response of *Meloidogyne incognita* to wet-dry cycles (Couch and Bloom, 1960) is further evidence of the probable importance of exudation rates or exudate quality on the behavior and reproductive success of these feeders. Filtrates of media from soil bacterial cultures containing low-molecular-weight organic acids have proven toxic to soil nematodes (Sayre, 1971). Thus changes in root-exudation quality or quantity, acting via changes in microbial growth, could influence nematode populations. Good (1968) noted several occasions in which wet-dry cycles were more effective in controlling nematode numbers than a milder crop-management technique, such as summer fallow.

Nematode population responses have been extensively reviewed by

Seinhorst (1970). He notes varying phytophagous nematode-population responses depending on their proximity to susceptible, resistant, or neutral host plants. Furthermore, life-history features of the populations in question are very important. A sedentary population with synchronous generations has a much different response from that of a continuously multiplying population. Many of the species have a generation time of less than one month, so that there is a high potential for extensive population increase under favorable conditions (Nielsen, 1949).

Spatial heterogeneity is important both in laboratory and field conditions; evidence of patchiness or clumped distributions were observed by Dalmasso (1968) for *Xiphinema* and *Longidorus*, both of which are present at the study area of the Central Plains Experimental Range where we have worked (Smolik, unpubl.).

In addition to the short-term, daily, .or weekly responses, nematodes responded to seasonal phenological events. Clumped nematode populations may display a lag before attacking new roots that grow very early (*i.e.*, one month before the shoot growing season) or during the burst of growth in late fall (Ares, 1976).

Feedback effects derived from phytophagous nematodes may also exert benefits for man-managed systems. Root systems of certain rice varieties are so well adapted to invasion by *Radopholus oryzae* that in its absence the rice will tiller excessively, markedly lowering yield (Seinhorst, 1961).

Effect on Individual and Population Function: Biochemical Effects

The second major event to be considered when evaluating the herbivory process is the introduction of biologically active substances into plants. These substances may be synthesized by the herbivores or passively carried. It is well known that insects can transfer viruses from one plant to another, and that these viruses may be detrimental to the plant's survival and reproduction. In addition, several insect species either produce plant hormones, such as auxins or gibberellins, or are important in transferring them from one tissue to another in a plant or from plant to plant (Miles, 1964, 1965, 1968, 1972; Hori, 1976; Hori and Endo, 1978).

SALIVA. Of recent interest is the role and importance of mammalian herbivores in introducing growth factors to a plant via saliva. Vittoria and Rendina (1960) suggested that thiamine in ruminant saliva may increase grass growth. Reardon *et al.* (1972) originally reported increased yields of *Bouteloua curtipendula* by treatment with bovine saliva added to the cut ends of leaf blades or by thiamine added to the soil, but saliva had no statistically significant effect on growth in a subsequent experiment (Reardon *et al.*, 1974). Similarly, bovine saliva reportedly had no effect on yield or tiller production of two species of *Festuca* (Johnston and Bailey, 1972). Reardon and Merrill (1978) later reported that both bovine saliva and thiamine enhanced *B. curtipendula* growth and that this effect was evident primarily when plants were subjected to detrimental environmental conditions, such as drought and low soil fertility. However, several experimental flaws exist in both programs.

We performed a variety of experiments to determine whether the growth or metabolism of *Bouteloua gracilis* was affected by potentially growth-promoting substances in the saliva of North American bison (*Bison bison*) (Detling *et al.*, 1980). When whole saliva was applied to clipped and unclipped plants, there was no significant effect ($p < 0.05$) of saliva on either net photosynthesis or root respiration over a 10-day period (Figure 11). During the 10-day experiment plant biomass was reduced by clipping but not affected by saliva (Figure 12). In a more detailed experiment (Detling *et al.*, unpubl.) we examined the effect of saliva on the distribution of photosynthetically fixed ^{14}C among leaf blades, leaf sheaths, crowns, and roots of *B. gracilis* clipped to heights of 6 cm (light), 4 cm (moderate), and 2 cm (heavy). There were no significant differences in carbon allocation patterns among the saliva- and non-saliva-treated plants (Figure 13). Similarly, leaf, crown, and root growth, as well as tiller production, were studied over a 10-week period. Both biomass and tiller production generally declined with increasing levels of defoliation (especially in the moderate and heavy treatments), and, again, there were no apparent saliva effects (Figure 14).

Finally, we (Detling *et al.*, unpubl.) examined the hypothesis of Reardon and Merrill (1978) that any potential saliva effects are more evident in nutrient-stressed plants than in nonstressed plants. Hydroponically grown *Bouteloua gracilis* plants were cultured for three weeks in one-seventh strength Hoagland's solution. Plant nitrogen stress was imposed by reducing the solution's nitrogen concentration from 2.14 mM to 0.42 mM. Control plants received unaltered one-seventh strength Hoagland's solution. Biomass and tiller production of nitrogen-stressed plants were about one-half those of nonstressed plants (Table 1). There was a slight, but statistically nonsignificant ($p < 0.05$), tendency for the saliva-treated plants from both nutrient treatments to produce more tillers than those not receiving saliva. Although the saliva-treated clipped plants from both nutrient groups produced slightly more biomass than those not receiving saliva, the opposite trend was observed in nonclipped plants. In neither case were these biomass differences significant ($p < 0.05$). Thus in our laboratory experiments the major effects of simulated grazing appear to have resulted from defoliation, and we have been unable to identify statistically significant effects from whole bison saliva.

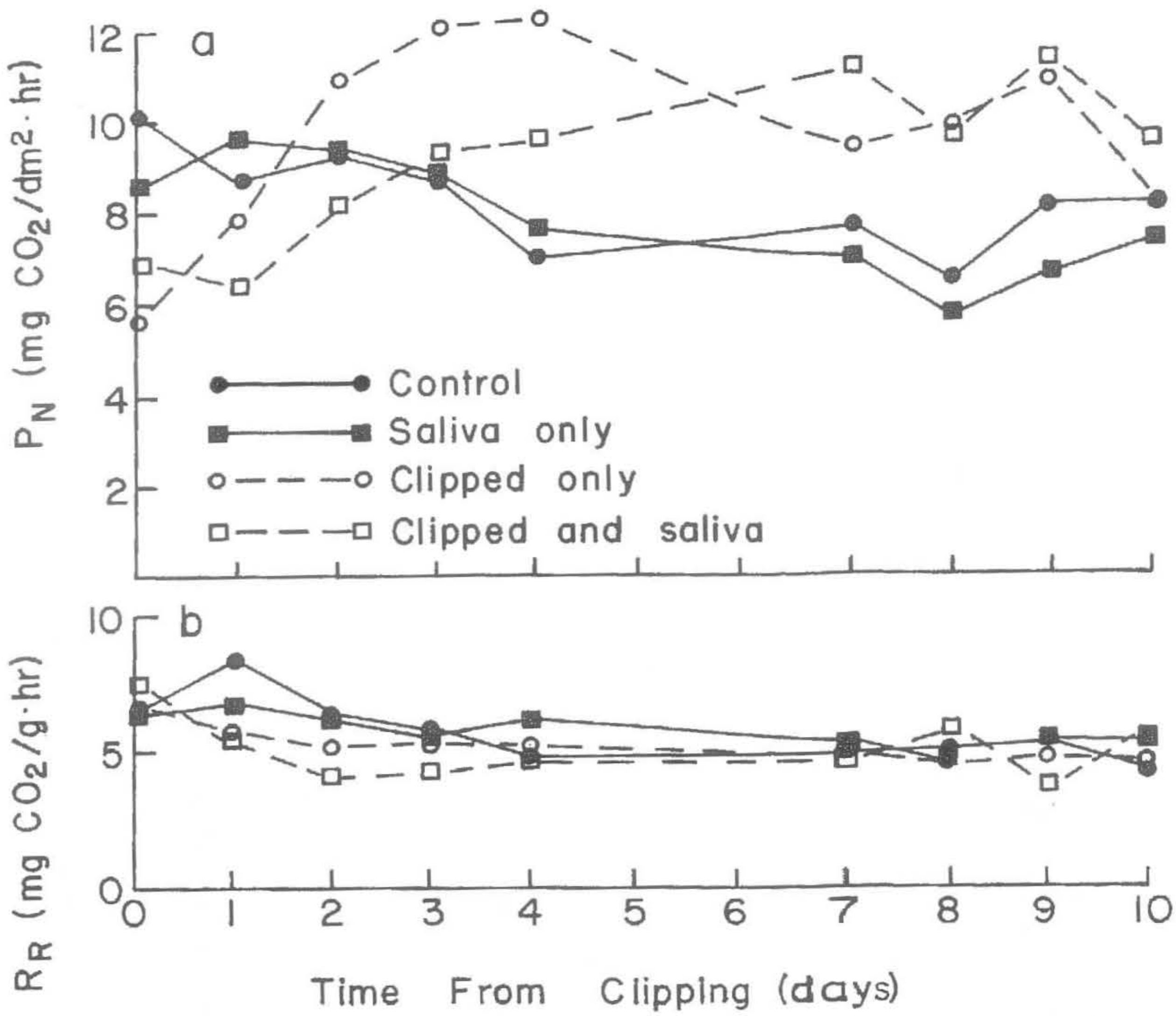

FIGURE 11. Net photosynthesis and root-respiration rates of *Bouteloua gracilis* defoliated with or without the addition of whole saliva from North American bison (Detling *et al.*, unpubl.).

STEROIDS. The effect of corticosteroids on plant growth has been examined intensively by several researchers in the past decade and a half and recently has been reviewed in depth by Heftmann (1975a, b). Leshem and coworkers in Israel (1967, 1969, 1972) reported that human chorionic gonadotropin promotes adventitious root production in various plants, and Geuns (1978) conclusively showed the widespread occurrence of natural steroid hormones in plants. Their activity is questioned in all cases because many of the experiments could not be repeated (Heftmann, 1975a), possibly because of the poor solubility of steroid hormones in water, making them very difficult to handle in experimental conditions. Nonetheless, several authors (Heftmann, 1975a; Geuns, 1978; and Leshem *et al.*, 1972) have noted the value of continuing research in this area.

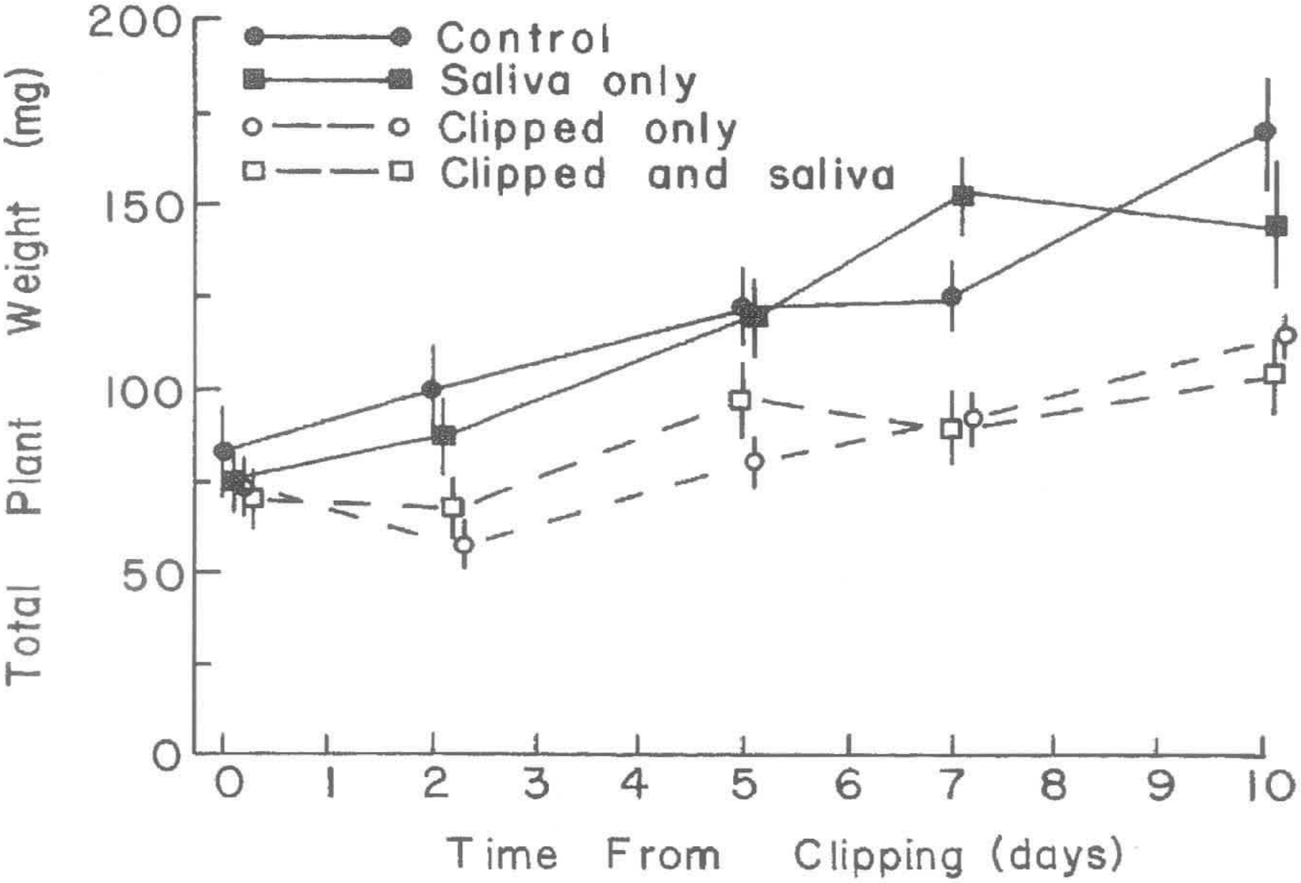

FIGURE 12. Total plant growth of *Bouteloua gracilis* following clipping with and without addition of whole saliva from North American bison (Detling *et al.*, unpubl.).

GROWTH FACTORS. One of the most heuristically interesting and intensely developing areas in medical and veterinary research concerns the existence and function of a relatively large class of extremely active compounds termed *growth factors*. Perhaps the best known of these is the Epidermal Growth Factor (EGF), a polypeptide serendipitously discovered by Cohen (1962) from mouse submaxillary gland. Several other classes of growth factors have since been found, purified, and described (cf. Gospodarowicz and Moran, 1976; Gospodarowicz *et al.*, 1978; and Hollenberg, 1976, 1980). Uniformly, these compounds demonstrate extreme biological activity, EGF showing greater activity in some cell culture systems than insulin (Hollenberg and Cuatrecasas, 1973, 1975). These compounds appear to be agents in the biochemical impact of herbivory. They are (1) hormonelike, having hyperactivity levels of $10^{-11}-10^{-10}$ M in animal cell cultures; (2) they are highly mitogenic, i.e., they stimulate both DNA and RNA synthesis in human fibroblasts (Hollenberg and Cuatrecasas, 1973); and (3) they may be produced widely in vertebrate systems, most commonly in the salivary glands and epithelial lining of the digestive system (Hollenberg and Gregory, 1976; Hollenberg, 1980). Un-

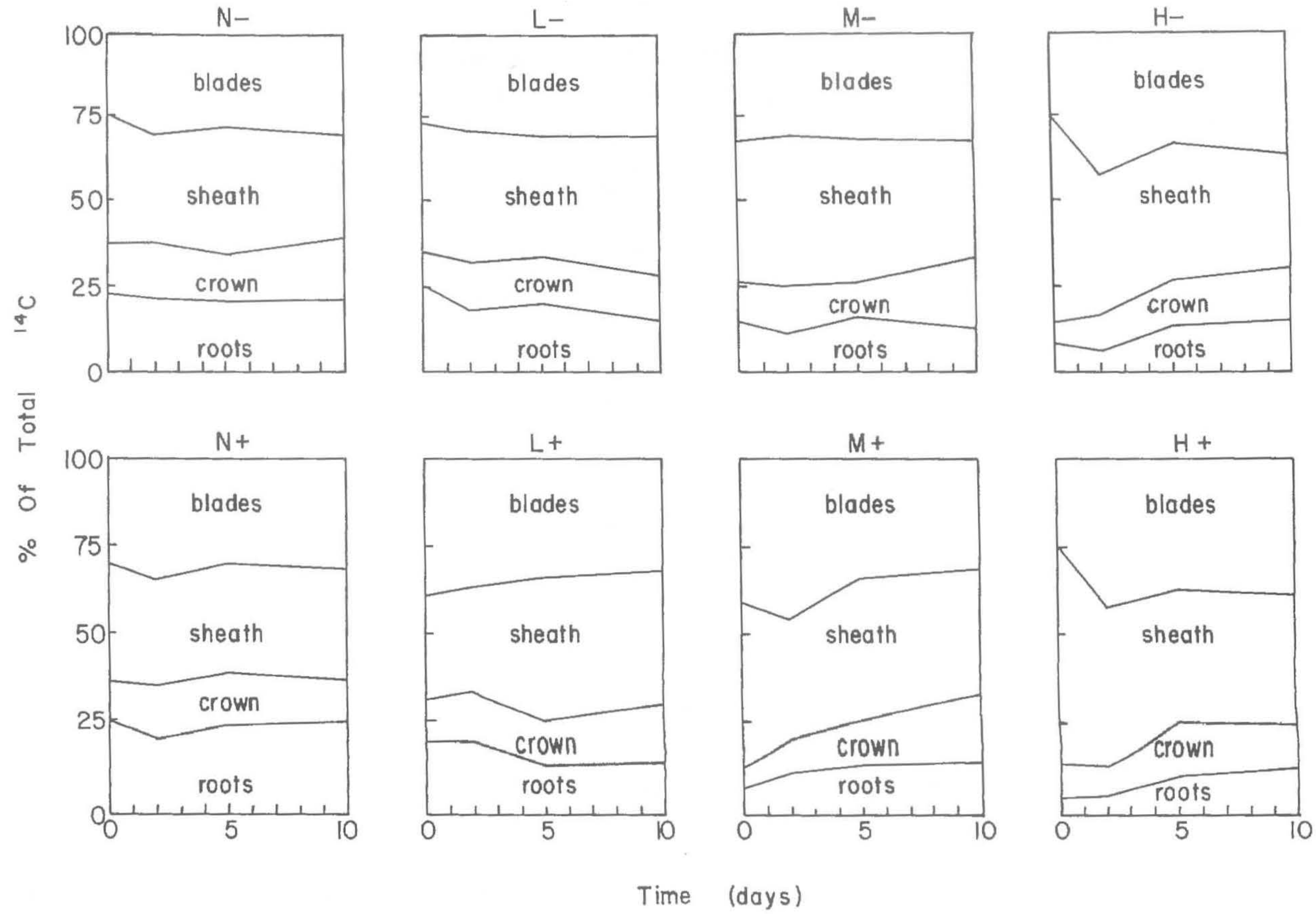

FIGURE 13. Distribution of photosynthetically fixed ^{14}C among plant parts of *Bouteloua gracilis* after no (N), light (L), moderate (M), or heavy (H) defoliation with (+) or without (−) whole bison saliva (Detling *et al.*, unpubl.).

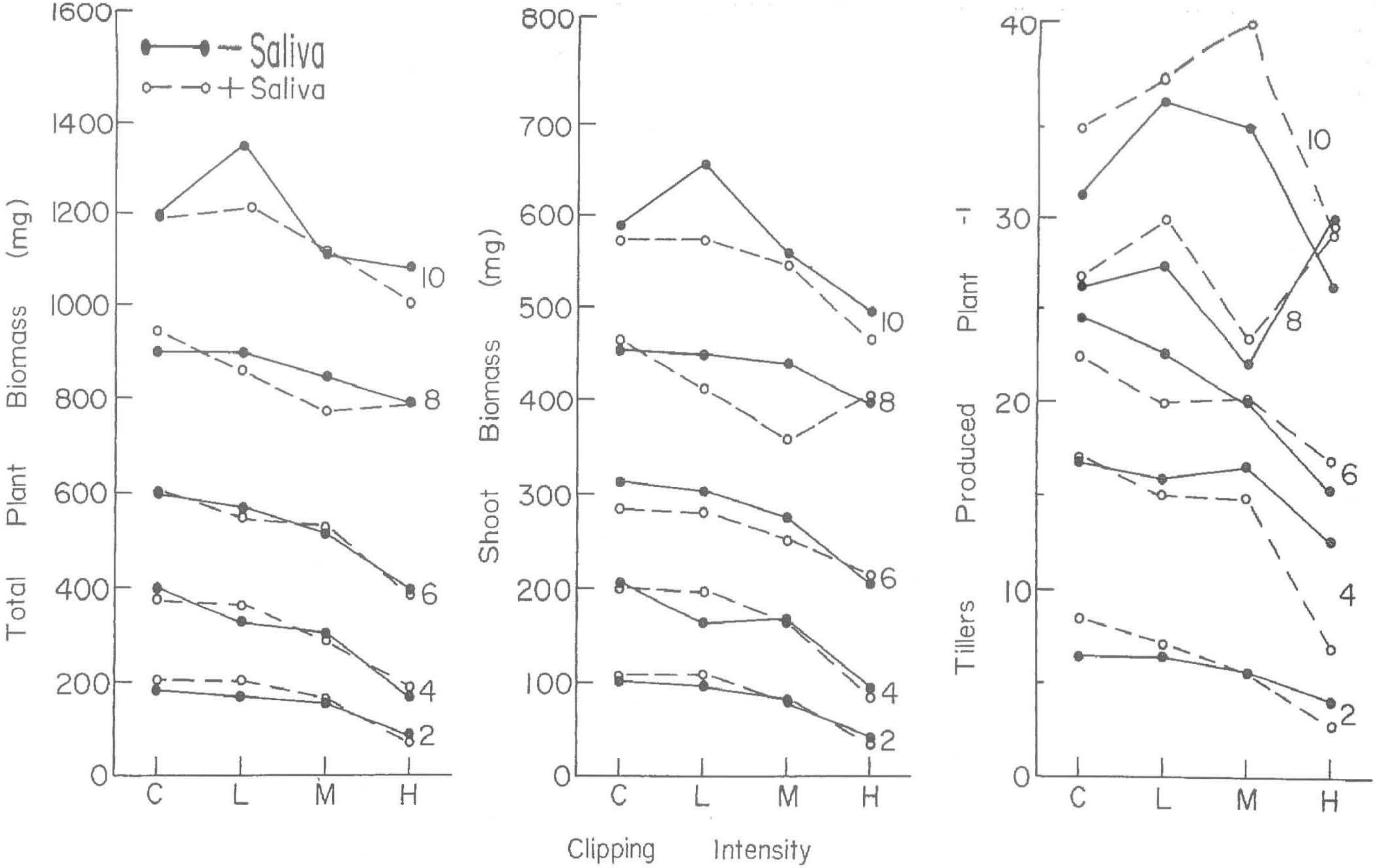

FIGURE 14. Growth and tiller production of *Bouteloua gracilis* with and without saliva. Numbers on the top of each figure represent weeks after no (N), light (L), moderate (M), or heavy (H) defoliation (Detling *et al.*, unpubl.).

TABLE 1. Interactive effects of clipping to 4 cm, nitrogen stress, and bison saliva. Each value is mean ($n = 12$) ± 1 S.E. (Detling *et al.*, 1980).

	Treatment	Tiller Production (per plant)	Final Biomass (mg/plant)				
			Live Leaves	Dead Leaves	Crown	Root	Total
N-stressed	Unclipped, no Saliva	10 ± 1	136 ± 19	46 ± 4	74 ± 9	131 ± 16	387 ± 43
	Unclipped, with Saliva	12 ± 1	116 ± 13	56 ± 5	64 ± 9	131 ± 17	367 ± 37
	Clipped, no Saliva	5 ± 1	83 ± 6	33 ± 3	48 ± 3	95 ± 4	259 ± 12
	Clipped, with Saliva	8 ± 1	79 ± 5	36 ± 3	50 ± 4	112 ± 8	277 ± 16
Non-N-stressed	Unclipped, no Saliva	26 ± 3	477 ± 51	41 ± 6	106 ± 14	261 ± 29	885 ± 94
	Unclipped, with Saliva	29 ± 3	387 ± 33	54 ± 9	113 ± 10	215 ± 22	769 ± 69
	Clipped, no Saliva	20 ± 3	246 ± 24	28 ± 4	72 ± 9	143 ± 13	490 ± 47
	Clipped, with Saliva	21 ± 3	272 ± 38	22 ± 4	102 ± 13	152 ± 16	548 ± 66

fortunately, little is known of the distribution of these compounds or the response of plant systems to their presence.

Although we have obtained conflicting data on biochemical effects using whole saliva, recently obtained data strongly suggest that growth factors isolated from mouse submaxillary glands stimulate plant growth (Dyer, unpubl.). For this study purified human Epidermal Growth Factor (EGF) was obtained from Collaborative Research, Waltham, Massachusetts, in crystalline form, reconstituted in water, and used at $3.9 \times 10^{-7} + 10^{-6}$ M in a standardized bioassay using the growth rate of seedlings as a measure of biological activity. Seeds of sorghum, mustard, corn, and tomato were germinated in distilled water, held in Hoagland's solution for three days, then treated with EGF, and monitored at three and six days after treatment. General aspect, relative length of roots, and the measured length of the shoots constituted the bioassay. Evidence from three replicated experiments using sorghum seedlings (Dyer, unpubl.) show that EGF increases shoot growth significantly over both 3-day and 6-day test periods. At three days growth was increased nearly 10% above untreated controls; growth enhancement declined to 4.5% for the 6-day trial. The general observations revealed that root growth was somewhat greater at 3 days but not apparently different at 6 days. Mustard leaf growth was slightly enhanced, but by six days no visual difference could be ascertained; there was no apparent effect on cornshoot or tomato-seedling growth, based on one trial each. Clearly, more work with growth factors is required, but at least some plant species appear to contain the necessary receptor systems to recognize some growth factors, and for short periods of time certain of their growth processes may be stimulated.

In addition to man, growth factors are known from several vertebrates, including ungulates and rodents (Hollenberg, 1980). EGF has been found in serum and urine. Because it is produced in the epithelial tissue of the esophagus, it may be present in feces as well. With the aid of M. D. Hollenberg we found that bison urine contains large amounts of EGF, although urine from a male mule deer (*Odocoileus hemionus*) was negative (Dyer *et al.*, unpubl.). We have also discovered, but not yet confirmed, a substance that is probably EGF in grasshopper oral exudates and crop contents, although our information to date indicates that it is not present in the salivary glands (Dyer *et al.*, unpubl.). This is the first report of such a growth factor in insects.

Effect on Community and Ecosystem Function

Much of the grazing-oriented or defoliation literature to which we have alluded or on which we have commented directly addresses range-management recommendations concerning short-term grazing intensities in terms of the number of animals that an area can sustain during the growing season and postgrowing season, or it addresses pest associations when large populations of phytophagous vertebrates or invertebrates invade an area. Few references give precise data concerning population, community, or ecosystem values from which optimal levels of grazing can be extrapolated. One exception is that provided by Vickery (1972), who studied sheep pastures stocked at three densities and discovered, from examining CO_2 exchange rates, that the pasture with medium densities outproduced those that were lightly or heavily stocked. NPP values for the medium-stocked pasture were 40% higher than those for the lightly stocked one and 29% higher than those for the heavily stocked one. There were seasonal variations as well, and early-spring conditions increased the potential for NPP even more in the medium-density pastures. This information gives some of the clearest evidence for the herbivore optimization concept discussed below.

Field corn subjected to redwing blackbird (*Agelaius phoeniceus*) foraging showed similar results for corn-grain biomass (Dyer, 1973, 1975). Simulation experiments suggested that corn compensates for lost tissue by increasing amino-acid production as well as biomass, although no information exists related to actual grazing pressure (Dyer, 1976). More recent experiments on corn (Arguello, 1978; Dyer and Arguello, unpubl.) show that *Zea* can compensate for up to 50% of the corn-ear tissue lost during mechanically simulated herbivory up to and exceeding 13% of the grain biomass on each growing ear. These data definitely show that the ability to compensate is related to the amount of plant tissue removed during the experiment, again following the general model of the herbivore optimization curve (Figure 15). These experiments were modified by the addition of whole bison saliva in order to ascertain any effects of a biomechanical plus biochemical interaction. In these instances productivity was significantly reduced when compared to mechanical damage levels alone; thus the hypothesis of increased growth compensation was rejected. However, full assessment of the experiment strongly suggests that too much saliva (1.0 ml/ear) was added, and the reduction can possibly be explained by salt toxicity. Importantly, in the same field, interspersed with the experimental plots, many corn ears were damaged by house sparrows (*Passer domesticus*), and the affected plants showed dramatic increases in overall production of corn ears, averaging more than 15% over controls (Dyer and Arguello, unpubl.). Here again is an excellent example of major differences observed between true herbivory and simulated herbivory in experiments.

McNaughton (1976, 1979) and McNaughton *et al.* (above) have shown

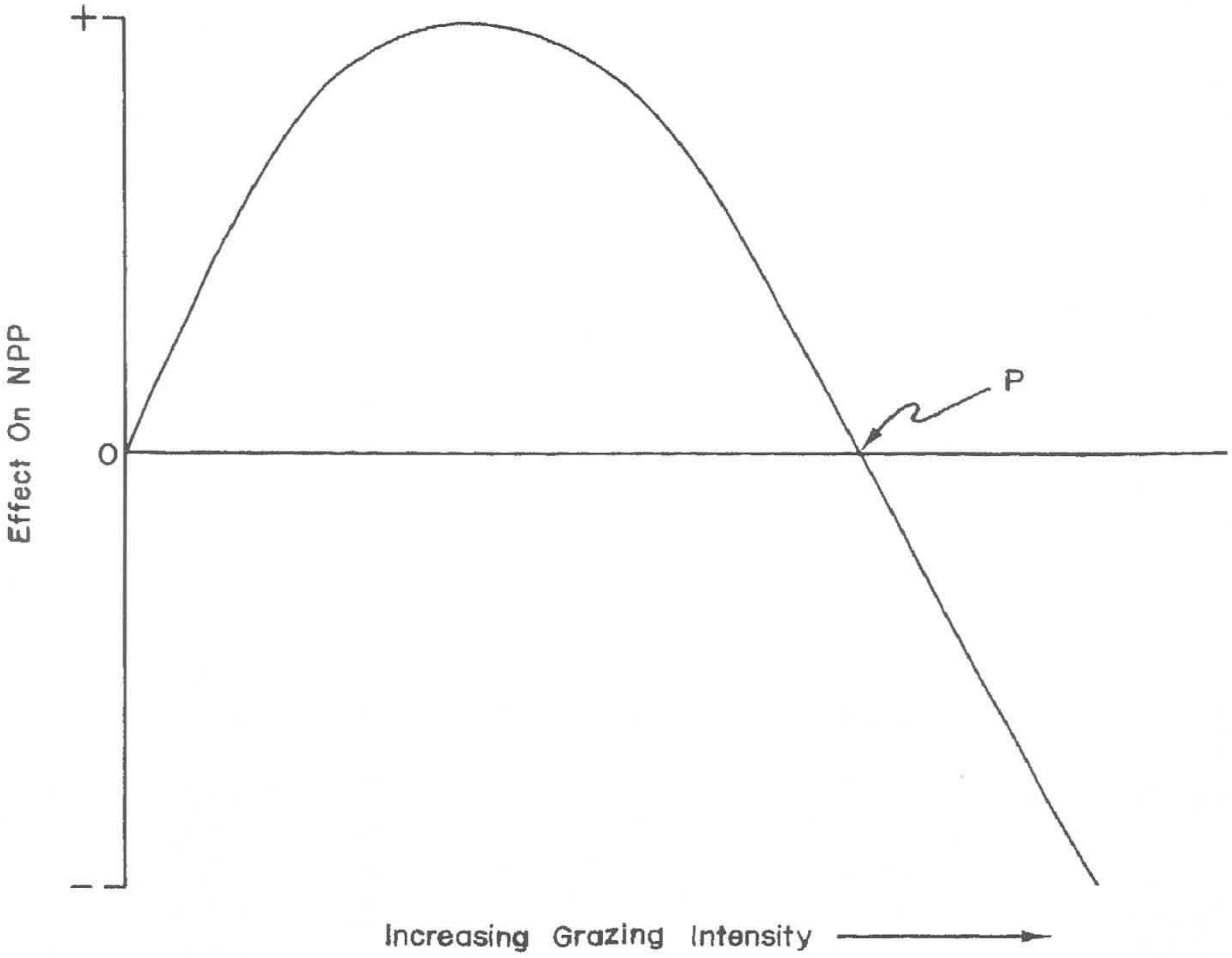

FIGURE 15. Herbivore Optimization Curve (after Dyer, 1975, and McNaughton, 1979). The hypothesis set by this relationship is that Net Primary Production is at first increased by herbivory, then reaches a maximum (at which there is optimum grazing intensity), and then declines to become negative as the plant is unable to compensate for lost tissue.

interactions between two large ungulate species and subsequent grass regrowth in the tropical savannahs of Africa. Indeed, from a total systems standpoint this information constitutes the best information collected to date defining and supporting the herbivore optimization concept. However, we have commenced studies along these lines in the North American grasslands and present our preliminary findings here.

The North American grassland ecosystem studied was a site in the Wind Cave National Park. This relictual Mixed-Grass Prairie was chosen because of the relative absence of human disturbance and because many of the native herbivore species range naturally through the area. The large herd complexes that McNaughton (1976, 1979) described from the

Serengeti naturally do not exist in the Wind Cave area; however, similar interactions do exist, e.g., between bison and prairie dogs (*Cynomys ludovicianus*). The information we have to date suggests that changes in the relative abundance of grasses and forbs in the prairie dog town areas are similar to those caused by prairie dogs alone as noted by Bonham and Lerwick (1976) and Hansen and Gold (1977). Plant diversity is slightly higher, and the standing crop is reduced, compared to other areas. Interestingly, although the towns occupy less than 5% of the park's area, the bison spend a significantly greater amount of their time (65%) per unit area in the town areas. Most of this time is spent in feeding.

Collections were made of western wheatgrass (*Agropyron smithii*) from prairie dog towns and from nearby areas that were seldom grazed by these animals. Although the standing-crop levels of the towns were about 50% of those of the nearby areas, protein levels were significantly higher, and the digestibility of the grass *in vitro* was also significantly higher. The tiller number per section of rhizome was also significantly higher, both in the field and in the greenhouse. Furthermore, initial screening in the laboratory and greenhouse strongly suggests that the plants from the two areas—the heavily grazed town area and the seldom grazed nontown area—may be genotypically different (Coppock, unpubl.). Studies are now being conducted to examine the degree to which each population responds to clipping.

PRODUCTIVITY INCREASE IN GRAZED ECOSYSTEMS—A MODEL

Herbivore Optimization Curve

Scattered reports of standing-crop averages suggest that under some circumstances plant response to herbivory results in a short-term increase in biomass and sometimes in protein (Dyer, 1976). Do these short-term responses affect long-term patterns? The answer to that question is complex and mixed. The relationship between net primary production and herbivory is expressed in a model known as the herbivore optimization curve (Dyer, 1973, 1975; McNaughton, 1976, 1979) (Figure 15). The model implies that the first response of the plant to herbivory is increased productivity with increased grazing intensity. It is obvious from both theoretical and empirical bases that any increases in plant growth response cannot continue unabated and a maximum potential is reached, probably quite often toward the lower end of the grazing intensity scale. Following the peak, it is estimated that plant production potential declines rapidly. The exact shape of the curve will probably be plant-animal association dependent, *i.e.*, dependent on associations with different functional forms. For some associations we expect the optimal point to be driven far to the right. Also, the magnitude of the productivity response should show considerable variation: in some instances there may be a very small curve that becomes apparent only with intensive study; in other instances the area under the curve may be very large.

Observations from different associations fit the model: grasslands (Vickery, 1972; McNaughton, 1976, 1979; Dyer, 1979) and agricultural crops, such as corn (Dyer, 1973, 1975, 1976), oats (Dawson, 1970), and carrot and beans (Scott, 1969, 1970, 1976). It appears that various conifers and broad-leafed deciduous trees respond negatively to insect attack (Harper, 1977), although contradictory information exists (Mattson and Addy, 1975). We still feel the key is an understanding of the level of herbivore attack upon the individual plant and within the community.

Examination of Growth Rates

If plants are capable of optimizing production following grazing, not only will absolute growth rates increase at certain levels of defoliation, but also relative growth rates will necessarily increase. Hilbert *et al.* (unpubl.) have used traditional plant-growth analysis (Blackman, 1919; West *et al.*, 1920; Kvet *et al.*, 1971) to address the question, how great a change in relative growth rate is necessary to increase primary production at a given level of grazing? The answer to this question will help clarify our thinking regarding the effects of herbivores on primary production and will suggest circumstances under which optimization of primary production can most likely be expected.

The relative growth rate of a plant (r) is defined (Kvet *et al.*, 1971) as

$$r = \frac{1}{w} \cdot \frac{dw}{dt} \tag{2}$$

where w is the dry weight of the plant or plant part and t is time.

In practice, the mean relative growth rate can be calculated from actual plant growth data by:

$$r = \frac{\ln w_2 - \ln w_1}{t_2 - t_1} \tag{3}$$

where w_1 and w_2 are plant weights at times t_1 and t_2 respectively. If grazing results in a change (Δr) in the plant's relative growth rate, its relative growth rate following grazing is expressed as the quantity

$$(r + \Delta r) \tag{4}$$

Hilbert *et al.* (unpubl.) have shown that, in order for the production of grazed plants to exceed that of ungrazed plants over a given period (Δt), the following inequality must hold true.

$$(r + \Delta r) > \frac{\ln \dfrac{(e^{r\Delta t} - G)}{t}}{\Delta t} \qquad (5)$$

Where G is the proportion of the biomass removed by grazing. We emphasize that Equation 5 does not predict how a plant will respond to grazing, but only how it must respond for its production to exceed that of an identical ungrazed plant.

When we express Equation 5 as an equality we can define the boundary condition along which the productivities of the grazed and ungrazed plants are identical. One such possible boundary line is plotted for various grazing intensities in Figure 16 together with the response of a hypothetical plant. An optimization curve will result in this example, with production being optimized at the grazing intensity where the plant's relative growth-rate response is at the highest point above the boundary line (point a in Figure 16). The greatest grazing intensity at which production is not decreased occurs where the two curves intersect (point b in Figure 16). Thus it is possible that a plant may respond to grazing with an increased relative growth rate, yet still have a relative growth rate ($r + \Delta r$) below the boundary line and hence produce less than an ungrazed plant over the same time interval. The latter response has been noted experimentally on several occasions (Ryle and Powell, 1975; Detling *et al.*, 1979).

To determine how a grassland plant would respond to defoliation in terms of Equations 2–5, we performed a defoliation experiment with 40-day-old seedlings of *Bouteloua gracilis*. Plants were defoliated at 6, 4, and 2 cm heights, removing 18%, 42%, and 70% of the shoot biomass, respectively. Ten plants from each treatment were destructively sampled for dry-weight determination on the day of treatment and again 14 days later. Mean-shoot relative growth rates were calculated from Equation 3, and the boundary line was calculated from growth rates of control plants using Equation 5. Results of this experiment (Figure 17) reveal that the increased relative growth rates of shoots following defoliation at the light and moderate levels were sufficient for these plants to outproduce the ungrazed controls over the time interval. Although the relative shoot growth rate of the heavily defoliated plants was slightly higher, it was below the value necessary to increase production over that of the unclipped controls.

In a more thorough analysis Hilbert *et al.* (unpubl.) have found that the precise shape of the boundary curve is a complex function of the three

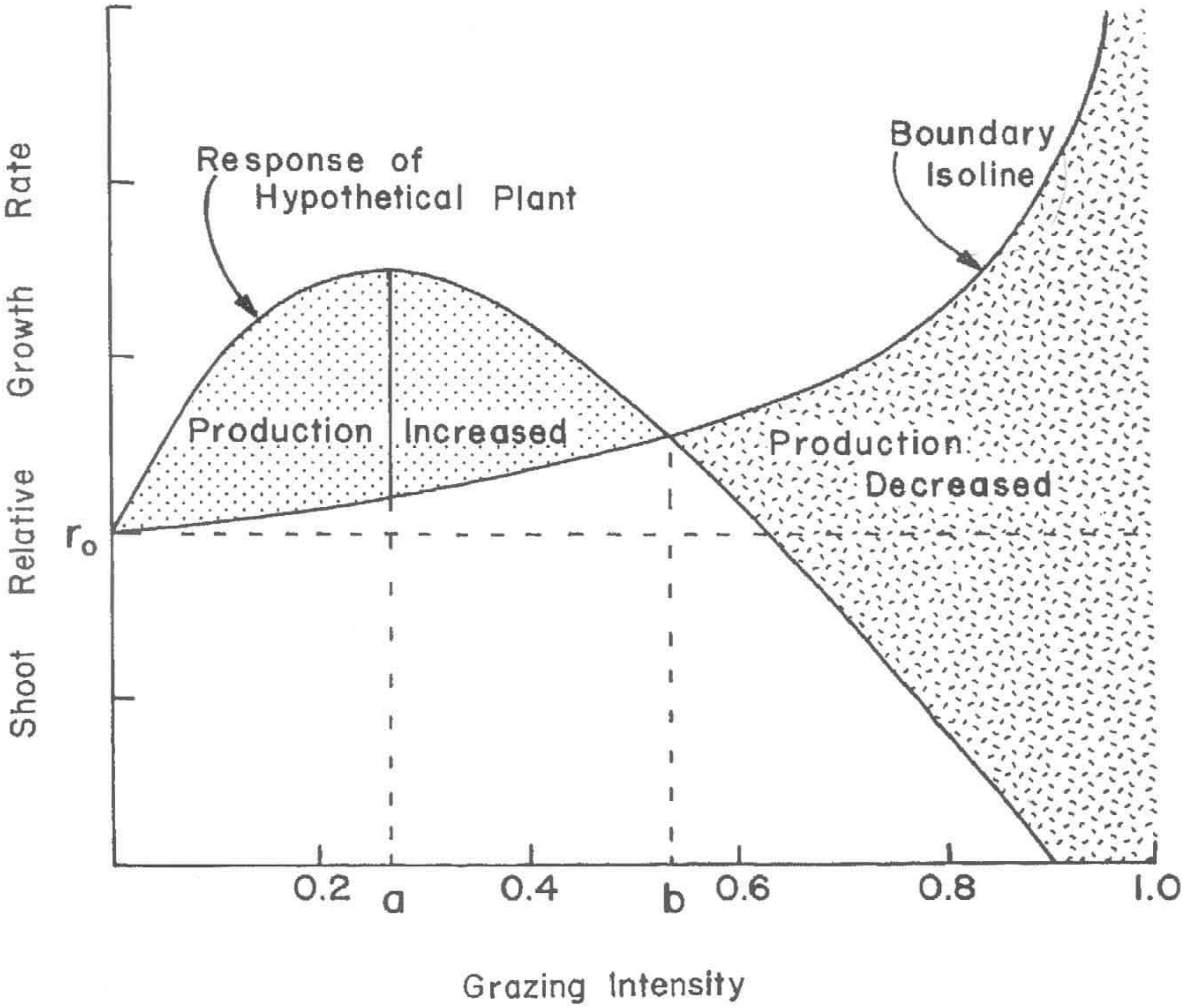

FIGURE 16. Plot of the boundary condition (relative growth rate) at which production of a grazed plant will equal that of an ungrazed plant at various grazing intensities (G). G_{opt} and G_{max} represent, respectively, the grazing intensities at which primary production is maximized and the maximum sustainable grazing intensity beyond which production decreases.

variables: r, G, and t. For example, while a given increase in relative growth rate following grazing is insufficient to increase production during one time interval, it may be sufficient if more time is permitted for recovery. Similarly, plants growing near their maximum potential relative growth rate (Grime and Hunt, 1975) can potentially sustain less grazing than plants with growth rates further below their maximum potential.

COEVOLUTIONARY ASSOCIATIONS IN GRASSLANDS

Perhaps one of the most interesting problems posed by our previous discussion is how would an association arise between plants and animals that

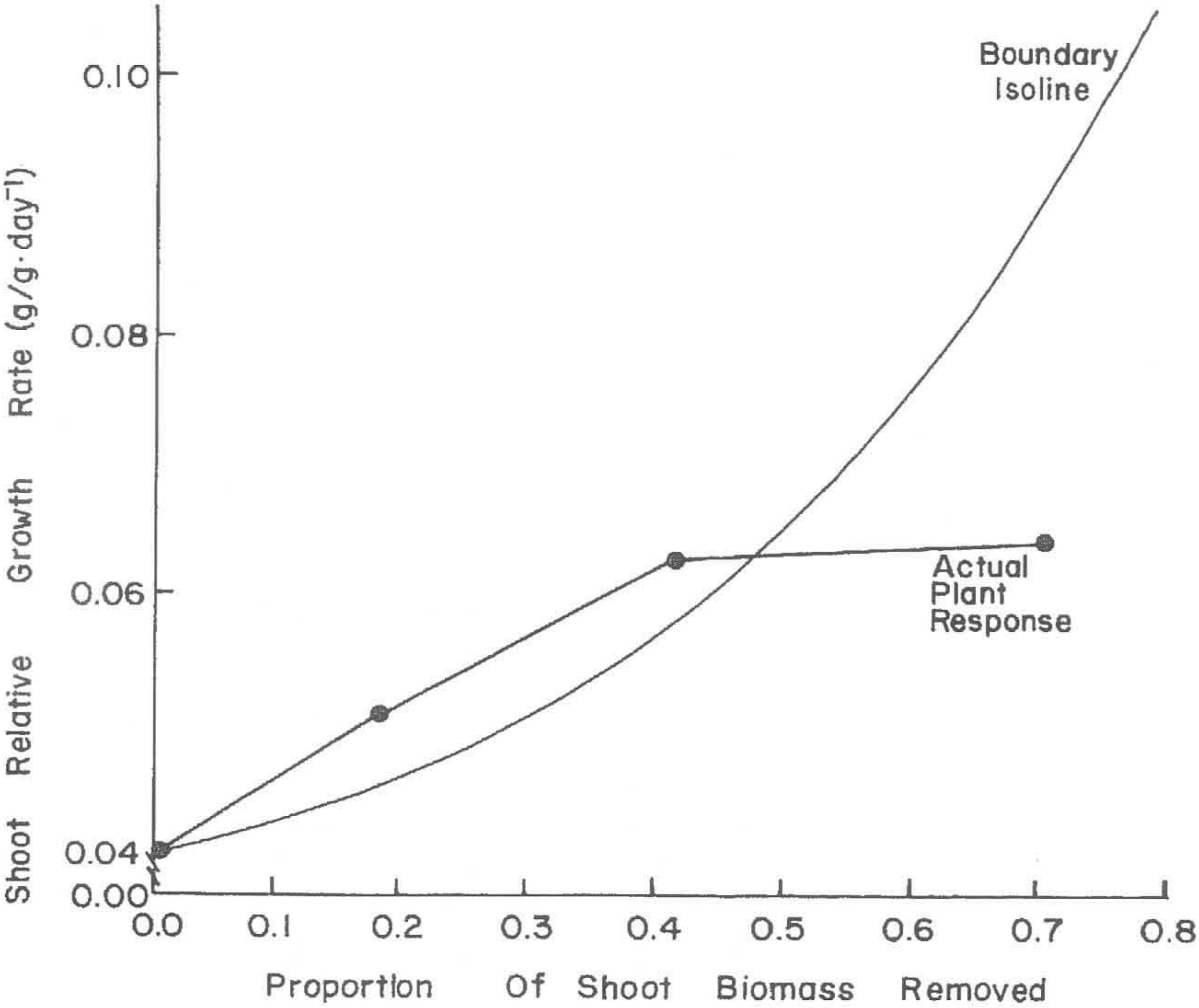

FIGURE 17. Plot of boundary line and actual data points obtained from *Bouteloua gracilis* plants defoliated at different levels.

benefits each in the way we postulate? With scant evidence, and mostly on the basis of *a priori* reasoning, Dyer and Bokhari (1976) and McNaughton (1976) assumed that plants and animals show these production phenomena as a result of coevolutionary interactions. Certainly it is easy to imagine that animal species have evolved various processes that function optimally, based on advantages to the individual in terms of carbon-flow dynamics, but it is more difficult to view the plant in the same perspective. Even though many biologists have noted the reactions in terms of production decreases, few, if any, have attempted to construct evolutionary hypotheses. Our basic hypothesis requires an expansion of the herbivore optimization curve to include well-known dynamics that are related to production of antiherbivore deterrents: secondary compounds; such structures as thorns and spines; thick or extremely hard tissue that is difficult to bite, chew, or digest; and, possibly, life-styles that

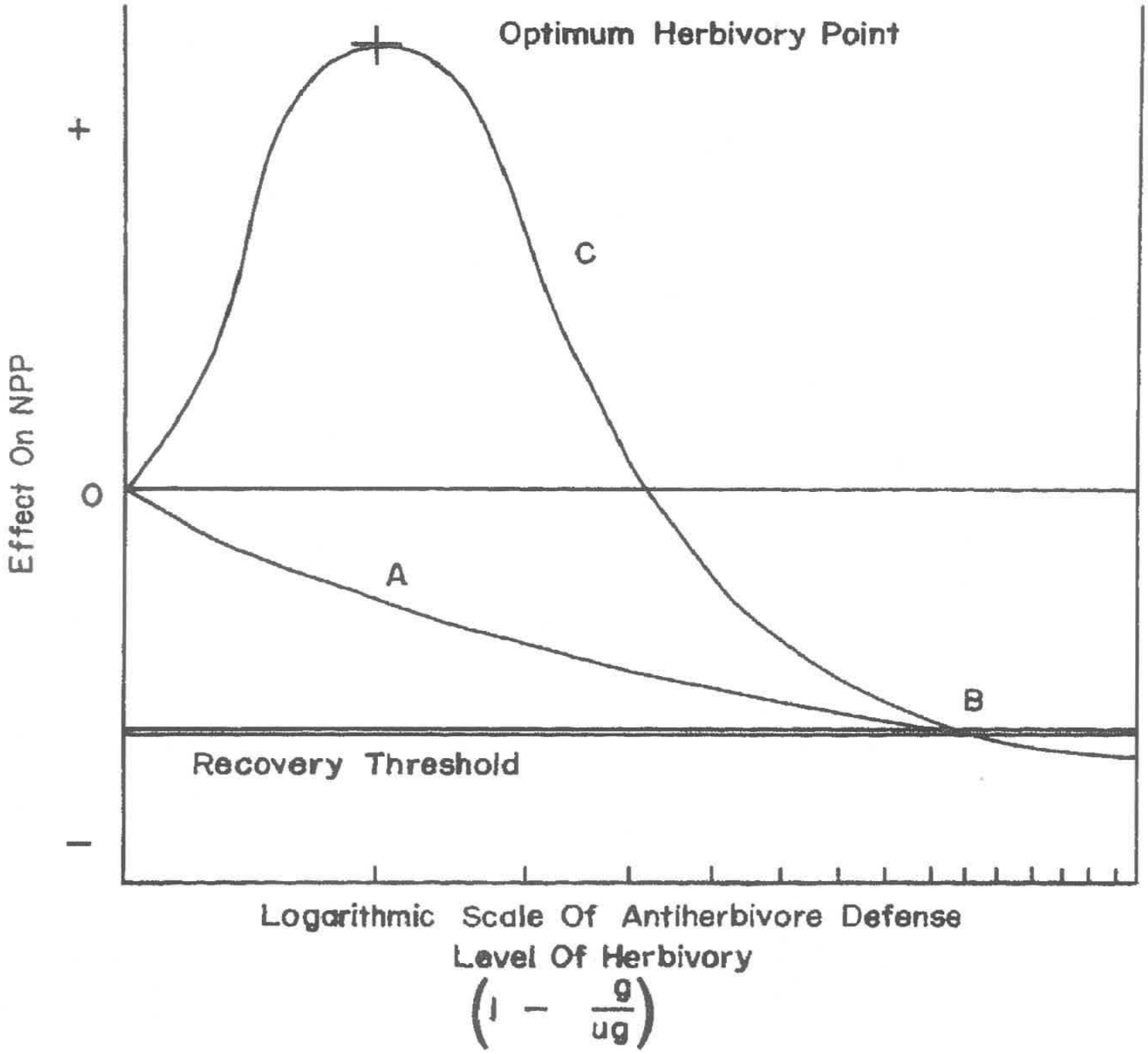

FIGURE 18. Theoretical model coupling Herbivore Optimization Concept with concepts about production of antiherbivore defenses in various plant species as a response to herbivory.

in some way preclude herbivore attack. Our reasoning is simple: We pose the hypothesis that, because many of these evolutionary strategies are energy-expensive (Seigler and Price, 1976; Jones, 1979), plants that couple increases in productivity as a function of herbivory with other protective mechanisms may, in the long run, be the most fit; although biologists noting this type of phenomenon have been most reluctant to attribute an increase in fitness to such responses (Simberloff *et al.*, 1978). Our hypothesis is shown in Figure 18.

We start with the herbivore optimization curve, as structured previously. The new arguments and assumptions that we make are the following:

(1) In order to contrast two hypothetical production conditions, we first consider plants that do not have the ability to increase productivity as a function of herbivory (Curve *A*). This hypothesis is the conventional viewpoint. Under these conditions lack of herbivory is the most advantageous herbivory level. Any herbivore attack on the plant can be deemed undesirable, and the greater the extent of herbivory to the single plant—either large amounts removed in single events or small amounts removed in several events over a longer period of time—the more adverse the condition. In this assessment, the sum of all herbivore attacks becomes the statistical measure of herbivory for any given community.

(2) We further assume there is a threshold (*B*) beyond which the individual plant cannot recover; and, collectively, if this is the threshold for all individuals, the plant population is at risk beyond that point. This simply says that, as curve *A* intercepts the threshold, individual plants die, and that community becomes locally extinct. It seems reasonable to argue that genotypes that are subjected to herbivory levels between *O* and the intercept of *A* and *B* and can lessen the attack level by antiherbivory defenses will be at a selective advantage (i.e., more fit). We note here that these defenses may require considerable energy to develop within any given individual, although Jones (1979) considers that this may not be so in all cases. Jones's argument is that we must know a great deal more about the metabolic function of the various plant compounds before making final judgments. We now draw attention to the herbivore optimization curve wherein the initial response of the plant is to increase rather than to decrease production levels. We have drawn in this curve (*C*) arbitrarily for the sake of producing a model, and, in so doing, we have driven the curve through the same threshold intercept as *A*. Now there is significant difference in energy available to the plant—the energy under the curves *A* and *C*—above the threshold of individual death or species extinction. Clearly, plants with option *C* have far more energy available to them for deploying various growth strategies, some of which may be directed toward antiherbivore defense.

Based on this model, we argue that plants showing the herbivore optimization curve would not direct a great deal of energy toward the production of plant defense mechanisms if, on the average, herbivory is at the optimal point set for the species. However, in a dynamic sense, this average position probably is seldom the case, and one should find considerable variability in the scheme within a species, on both proximate (ecological) bases and ultimate (evolutionary) bases within a community.

Those populations subjected to herbivory should show concomitant development of herbivore defense mechanisms. Whether such mechanisms are relaxed at the point of optimality or lower is a moot point; however, the converse should be true: if herbivore pressure exceeds the optimum level, there is obviously more energy flowing from the plants than can be compensated. At this point those plants that produce more deterrents should be more fit than their neighbors that have insufficient defenses. Note here that there is additional energy available to sustain all growth and maintenance and to provide for defense mechanisms that are energy expensive.

As herbivore pressure increases, there is an ever-increasing potential for selection for plants showing these two functions, a measure that for the sake of simplicity we show on a logarithmic scale (Figure 18). The point here is that the plant population to survive must produce deterrents to ward off or diminish herbivore attack.

In systems, such as grasslands, where herbivory is a dominant function, our model predicts the presence of a high proportion of the plant species that respond to herbivore pressures in this manner. With relaxation of herbivory there should be an invasion of plant species that lack these defenses against grazing, and possibly the invaders should replace or dominate the native taxa that continue to expend energy to produce antiherbivore defenses. McNaughton (1979) provides an excellent example of such a situation in the African Serengeti.

THE ROLE OF HERBIVORES IN GRASSLAND SYSTEMS

Considerable attention has been given to the function of animals in grassland systems, and herbivorous animals are typically considered to be regulators of the plant species in the systems and thus regulators of the system itself. Seldom, however, does this regulatory influence result in destruction of the system through overgrazing. As Hairston *et al.* (1960) suggested, the population of herbivores is controlled by predators and parasites rather than by food supply, although it is not clear that sufficient attention was given to either food quantity or food quality in their arguments. Harper (1977, p. 497) agrees with this assessment and states, ". . . plants in natural environments are seldom seen to suffer from animal damage." This comment seems to be especially true for grassland systems; perhaps in no other system are the predictable, steady, and high levels of grazing so apparent. In only a few instances can one cite situations where herbivory annihilated the total grassland vegetation, and those few cases were probably quite abnormal situations where man had intervened in some way.

Chew (1974), Owen and Weigert (1976), Harris (1974), Mattson and

Addy (1975), and Stenseth (1978) are some of the few workers to consider process-oriented functions wherein consumer functions are defined in a regulatory capacity. In a philosophical vein, Mattson and Addy (1975) considered that consumers function as *cybernetic regulators* in the system and in a sense make the system more predictable in its behavior. This is an interesting concept, and our impressions of function of both aboveground and belowground consumers exist within this conceptual framework. We believe that the biomechanical and biochemical processes discussed above are good candidates for the encoding process that enables plants to respond to herbivory by compensating for lost tissue. The biomechanical aspect is, without doubt, extremely important, but the biochemical process may be the more powerful. We tend to view it as functioning much like an electronic system where considerable gain is realized from a modest input. Time will tell whether this is a useful analogy.

In discussing any of the above phenomena, the area of greatest uncertainty is that of the biochemical effects, particularly the Growth Factors. We know, however, a great deal about plant responses to the physical environment, and we can place this information on a continuum as follows:

Light→CO_2→Water→Nutrients→Hormones (both plant and animal)→Growth Factors. (6)

Notice that in proceeding through the continuum a second scale is imposed, that of increased biological activity. Further, it seems to us there is an inverse correlation between our understanding of function at each level and inherent control function in the plant. By the time we come to Growth Factors we leave the realm of strong inference and enter that of speculation, especially considering a second dimension associated with the parameters, that of interactions. Here we are caught in an interesting bind between integration of facts and reductionism. We may not know plant-community function sufficiently well until we obtain a better understanding of these lesser-known subjects.

Experiments on the effect of herbivore-mediated Growth Factors in this area are exceedingly difficult to replicate. This is also the experience of workers studying the effects of steroidal hormones on plants. Another complication we have encountered is high variance, despite reasonably large sample sizes, in many of our experiments. Therefore, though we often obtain good evidence that treatment means are constantly higher than control means, they do not separate using parametric statistics. This could result from extreme genetic variation in the experimental plants.

Despite these difficulties we know that, within vertebrate species, Growth Factors, and the salivary glands thought to be producers of such factors, are under hormonal control. Androgens are especially important to EGF production and to control of yearly cycles of gland size and function in several species. We should expect circadian as well as circennial variations and control. The distribution of Growth Factors among herbivores is an interesting and important question. If the factors are of restricted distribution, then the plant/animal associations of paleograsslands constitute a second-level question of high importance. What of the production of Growth Factors among below-ground phytophagous systems? These questions may become important experimental issues, but our current state of knowledge is seriously deficient.

If vector-mediated biochemical messages are significant, then the mode of transport is equally significant. We can think of two primary models, one of which has a potential secondary variant:

1a. Plant-synthesized compounds are picked up by an animal and transported to another part of the plant or to another plant.
  b. Plant-synthesized compounds are picked up by an animal. These compounds then induce production of a new, animal-synthesized material that is then transported to other parts of the plant or another plant.
2. Animals produce regulatory compounds *de novo* and transport these on to the plant.

"If growth regulators are so important and so potent," it is reasonable to ask, "why isn't a greater effect observed in the system?" In order to avoid undue convolutions in our approach to this question, we simply argue that, while plants may be receptive to growth regulators manufactured and/or carried by consumers, the effects of regulators would be limited by interactions with other important components, such as nutrients, plant hormones, and water already within the plant. The most parsimonious viewpoint we can put forward is that the presence of animals and the introduction of growth regulators is simply a fine-tuning mechanism for the system. The presence of these compounds allows the plant to approach its full genetic capacity with respect to biological productivity. The biomechanical and biochemical stimuli may serve as cues that a plant can use to alter its growth functions and resource utilization. These, in the simplest sense, are the best set of candidates for animals providing the code as *cybernetic regulators* in the most classic sense.

Assuming for the moment that the biochemical impacts of herbivory do act as cybernetic regulators, then the lack of these compounds in any one growing season or over a period of several years would not be disastrous as far as an individual, the population, or perhaps a whole plant community is concerned. We, however, hypothesize that with continued long-term absence (decades and possibly centuries) there would be the chance that plant community structure would be affected. Obviously we cannot now know the manifestations of this possible effect, but we feel that overall productivity could be altered. Possibly changes in phenotype/genotype of various plant species could come about, and eventually the status of the entire plant community could change. Whether these ideas can even be tested is a controversial point at this time.

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